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ALHEIT, J., AND A. BAKUN.
1991. Reproductive success of sprat (*Sprattus sprattus*) in German Bight during 1987. Theme session on the Sardine-Anchovy Recruitment Project (SARP). 79th ICES Statutory Meeting, La Rochelle, France, September 26 - October 2, 1991. ICES DOC. C.M. 1991/L:44, 12 p. 910

ALVARIÑO, A.
1991. Abundancia y distribucion batimetrica diurna y nocturna de los sifonoforos durante las cuatro estaciones del año 1969, en aguas de California y Baja California. Inv. Mar. CICIMAR 6(2):1-37 [in Spanish with English abstract]. 9102

———.
1991. Chaetognatha. *In* K. G. and R. G. Adiyodi (eds.), Reproductive biology of invertebrates, p. 329-338. Volume VI, Part B: Asexual Propagation and Reproductive Strategies. Oxford & IBH Publishing Co. Pvt. Ltd., New Delhi. 9103

AU, D. W.
1991. Polyspecific nature of tuna schools: shark, dolphin, and seabird associates. Fish. Bull., U.S. 89(3):343-354. 9104

BAKUN, A., J. ALHEIT, AND G. KULLENBERG.
1991. The Sardine-Anchovy Recruitment Project (SARP): rationale, design and development. Theme session on the Sardine-Anchovy Recruitment Project (SARP). 79th ICES Statutory Meeting, La Rochelle, France, September 26 - October 2, 1991. ICES DOC. C.M. 1991/L:43, 18 p. 9105

———, AND C. S. NELSON.
1991. The seasonal cycle of wind stress curl in subtropical eastern boundary current regions. J. Phys. Oceanogr. 21(12):1815-1834. 9106

———, AND R. H. PARRISH.
1991. Comparative studies of coastal pelagic fish reproductive habitats: the anchovy, *Engraulis anchoita*, of the southwestern Atlantic. ICES J. mar. Sci. 48:343-361. 9107

———, C. ROY, AND P. CURY.
1991. The comparative approach: latitude dependence and effects of wind forcing on reproductive success. Theme session on the Sardine-Anchovy Recruitment Project (SARP). 79th ICES Statutory Meeting, La Rochelle, France, September 26 - October 2, 1991. ICES DOC. C.M. 1991/H:45, 12 p. 9108

TABLE OF CONTENTS (CONTINUED)

BALAZS, G. H.
1991. Sea turtle tag center of the Pacific. Mar. Turtle Newsl. 52:14-15. 9109

BARLOW, J.
1991. The utility of demographic models in marine mammal management. Rep. int. Whal. Commn 41:573-577. 9110

———, AND P. BOVENG.
1991. Modeling age-specific mortality for marine mammal populations. Mar. Mammal Sci. 7(1):50-65. 9111

BOEHLERT, G. W.
1991. Southwest Fisheries Science Center Honolulu Laboratory. *In* C. D. Becker (ed.), Fisheries Laboratories of North America, p. 147-148. Am. Fish. Soc., Bethesda, Maryland. 9112

———, M. KUSAKARI, AND J. YAMADA.
1991. Oxygen consumption of gestating female *Sebastes schlegeli*: estimating the reproductive costs of livebearing. *In* G. W. Boehlert and J. Yamada (eds.), Rockfishes of the genus *Sebastes*: their reproduction and early life history. Environ. Biol. Fishes 30:81-89.. 9113

———, M. S. LOVE, J. P. WOURMS, AND J. YAMADA.
1991. A summary of the symposium on rockfishes and recommendations for future research. *In* G. W. Boehlert and J. Yamada (eds.), Rockfishes of the genus *Sebastes*: their reproduction and early life history. Environ. Biol. Fishes 30:273-280. 9114

———, AND J. YAMADA.
1991. Introduction to the symposium on rockfishes. *In* G. W. Boehlert and J. Yamada (eds.), Rockfishes of the genus *Sebastes*: their reproduction and early life history. Environ. Biol. Fishes 30(1-2):9-13. 9115

BOGGS, C. H.
1991. Bioenergetics and growth of northern anchovy *Engraulis mordax*. Fish. Bull. 89(4):555-566. 9116

BUSHNELL, P. G., AND R. W. BRILL.
1991. Responses of swimming skipjack (*Katsuwonus pelamis*) and yellowfin (*Thunnus albacares*) tunas to acute hypoxia, and a model of their cardiorespiratory function. Physiol. Zool. 64(3):787-811 9117

BUTLER, J. L.
1991. Mortality and recruitment of Pacific sardine, *Sardinops sagax caerulea*, larvae in the California Current. Can. J. Fish. Aquat. Sci. 48(9): 1713-1723. 9118

TABLE OF CONTENTS (CONTINUED)

———, W. W. WAKEFIELD, P. B. ADAMS, B. H. ROBISON, AND C. H. BAXTER.
1991. Application of line transect methods to surveying demersal communities with ROVs and manned submersibles. Oceans 91 Conference Proceedings, Honolulu, Hawaii, October 1-3, 1991, p. 689-696. 9119

CALAMBOKIDIS, J., AND J. BARLOW.
1991. Chlorinated hydrocarbon concentrations and their use for describing population discreteness in harbor porpoises from Washington, Oregon, and California. *In* J. E. Reynolds III and D. K. Odell (eds.), Marine mammal strandings in the United States, p. 101-110. Proceedings of the Second Marine Mammal Stranding Workshop, Miami, Florida, December 3-5, 1987. NOAA Technical Report NMFS 98. 9120

CHIVERS, S. J., AND P. A. AKIN.
1991. Sampling effects on the estimation of life history parameters for eastern tropical Pacific dolphins. Rep. int. Whal. Commn 41:525-527. 9121

CONTE, F. P., K. TAKANO, A. TAKEMURA, AND G. W. BOEHLERT.
1991. Ontogeny of the sodium pump in embryos of rockfish of the genus *Sebastes*. Environ. Biol. Fishes 30(1-2):127-134. 9122

DAILEY, M. D., M. L. FAST, AND G. H. BALAZS.
1991. *Carettacola hawaiiensis* n. sp. (Trematoda: Spirorchidae) from the green turtle, *Chelonia mydas*, in Hawaii. J. Parasitol. 77:906-909. 9123

DAVENPORT, J., AND G. H. BALAZS.
1991. "Fiery bodies"—Are pyrosomas an important component of the diet of leatherback turtles? Br. Herpetol. Soc. Bull. 37:33-38. 9124

DeMARTINI, E. E.
1991. Annual variations in fecundity, egg size, and the gonadal and somatic conditions of queenfish, *Seriphus politus* (Sciaenidae). Fish. Bull., U.S. 89(1):9-18. 9125

DIZON, A. E., S. O. SOUTHERN, AND W. F. PERRIN.
1991. Molecular analysis of mtDNA types in exploited populations of spinner dolphins (*Stenella longirostris*). *In* A. R. Hoelzel and G. P. Donovan (eds.). Rep. int. Whal. Commn (Special Issue 13):183-202.. 9126

DUFFIELD, D. A., J. CHAMBERLIN-LEA, J. C. SWEENEY, D. K. ODELL, E. D. ASPER, AND W. G. GILMARTIN.
1991. Use of corneal cell culture for R-band chromosome studies on stranded cetaceans. *In* J. E. Reynolds and D. K. Odell (eds.), Marine mammal strandings in the United States, p. 91-100. Proceedings of the Second Marine Mammal Stranding Workshop, Miami, Florida, December 3-5, 1987.. 9127

TABLE OF CONTENTS (CONTINUED)

ELDRIDGE, M. B., J. A. WHIPPLE, M. J. BOWERS, B. M. JARVIS, AND J. GOLD.
1991. Reproductive performance of yellowtail rockfish, *Sebastes flavidus*. Environ. Biol. Fishes 30:91-102. 9128

FIEDLER, P. C., V. PHILBRICK, AND F. P. CHAVEZ.
1991. Oceanic upwelling and productivity in the eastern tropical Pacific. Limnol. Oceanogr. 36(8):1834-1850. 9129

FORNEY, K. A., D. A. HANAN, AND J. BARLOW.
1991. Detecting trends in harbor porpoise abundance from aerial surveys using analysis of covariance. Fish. Bull., U.S. 89(3):367-377. 9130

———, A. J. LEETE, AND D. G. LINDBURG.
1991. A bar code scoring system for behavioral research. Am. J. Primatol. 23:127-135. 9131

GERRODETTE, T.
1991. Models for power of detecting trends--a reply to Link and Hatfield. Ecology 72(5):1889-1892. 9132

———, AND P. R. WADE.
1991. Monitoring trends in dolphin abundance in the eastern tropical Pacific: analysis of 1989 data. Rep. int. Whal. Commn 41:511-515. 9133

GORDOA, A. C., AND J. E. HIGHTOWER.
1991. Changes in catchability in a bottom-trawl fishery for Cape hake (*Merluccius capensis*). Can. J. Fish. Aquat. Sci. 48:1887-1895. 9134

HEWITT, R. P., AND D. A. DEMER.
1991. Krill abundance. Nature 353:310. 9135

HOBSON, E. S.
1991. Hazardous aquatic organisms. Section 12, NOAA Diving Manual, 12:1-12. U.S. Dep. Commer., NOAA, U.S. Government Printing Office, Washington, D.C.. 9136

———.
1991. Trophic relationships of fishes specialized to feed on zooplankters above coral reefs. *In* P. F. Sale (ed.), The Ecology of Fishes on Coral Reefs, p. 69-95. Academic Press, Inc.. 9137

HOHN, A. A., R. B. MILLER, K. M. PELTIER, AND S. J. CHIVERS.
1991. Composition of the incidental kill of small cetaceans in the U.S. purse-seine fishery for tuna in the eastern tropical Pacific during 1989. Rep. int. Whal. Commn 41:493-496. 9138

TABLE OF CONTENTS (CONTINUED)

HOLT, R. S., R. P. HEWITT, AND J. E. ROSENBERG.
1991. The U.S. AMLR program: 1990-1991 field season activities. Antarctic Marine Living Resources (AMLR) program, p. 187-188. Antarct. J. U.S.. 9139

KOPE, R. G.
1991. Current analytic concerns with harvest-rate management. *In* T. J. Hassler (ed.), Proceedings of the 1990 Northeast Pacific Chinook and Coho Salmon Workshop, p. 45-55. California Cooperative Fishery Research Unit, Humboldt State University, Arcata, California. 9140

KLEIBER, P., AND C. PERRIN.
1991. Catch-per-effort and stock status in the U.S. North Pacific albacore fishery: reappraisal of both. Fish. Bull., U.S. 89(3):379-386. 9141

KRAMER, S. H.
1991. Growth, mortality, and movements of juvenile California halibut *Paralichthys californicus* in shallow coastal and bay habitats of San Diego County, California. Fish. Bull., U.S. 89(2):195-207. 9142

———.
1991. The shallow-water flatfishes of San Diego County. Calif. Coop. Oceanic Fish. Invest. Rep. 32:128-142. 9143

LAIDIG, T. E., S. RALSTON, AND J. R. BENCE.
1991. Dynamics of growth in the early life history of shortbelly rockfish, *Sebastes jordani*. Fish. Bull., U.S. 89(4):611-621. 9144

LENARZ, W. H., AND T. W. ECHEVERRIA.
1991. Sexual dimorphism in *Sebastes*. *In* G. W. Boehlert and J. Yamada (eds.), Rockfishes of the genus *Sebastes*: their reproduction and early life history, p. 71-80. Environ. Biol. Fishes 30(1-2):71-80. 9145

———, R. J. LARSON, AND S. RALSTON.
1991. Depth distributions of late larvae and pelagic juveniles of some fishes of the California Current. Calif. Coop. Oceanic Fish. Invest. Rep. 32:41-46. 9146

LOWRY, M. S., B. S. STEWART, C. B. HEATH, P. K. YOCHEM, AND J. M. FRANCIS.
1991. Seasonal and annual variability in the diet of California sea lions *Zalophus californianus* at San Nicolas Island, California, 1981-86. Fish. Bull., U.S. (Note) 89(2):331-336.. 9147

MacCALL, A. D.
1991. Southwest Fisheries Science Center Tiburon Laboratory. *In* C. D. Becker (ed.), Fisheries Laboratories of North America, p. 153-155. Am. Fish. Soc., Bethesda, Maryland. 9148

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MASON, J. E.

1991. Variations in the catch of jack mackerel in the southern California purse seine fishery. Calif. Coop. Oceanic Fish. Invest. Rep. 32:143-151. 9149

MOSER, H. G., AND G. W. BOEHLERT.

1991. Ecology of pelagic larvae and juveniles of the genus *Sebastes*. *In* G. W. Boehlert and J. Yamada (eds.), Rockfishes of the genus *Sebastes*: their reproduction and early life history. Environ. Biol. Fishes 30(1-2):203-224.. 9150

MYRICK, A. C., JR.

1991. Some new and potential uses of dental layers in studying delphinid populations. *In* K. Pryor and K. S. Norris (eds.), Dolphin Societies: Discoveries and Puzzles, p. 251-279. University of California Press, Berkeley and Los Angeles. 9151

PEARSON, D. E., J. E. HIGHTOWER, AND J. T. H. CHAN.

1991. Age, growth, and potential yield for shortbelly rockfish *Sebastes jordani*. Fish. Bull., U.S. 89(3):403-409. 9152

PERRIN, W. F.

1991. What can be done about conflicts between marine mammals and fisheries? *In* Proceedings of Symposium on Present Status of Marine Mammals in Taiwan, p. 21-35. Taiwan National Ocean University, Keelung, May 7, 1991.. 9153

———.

1991. Why are there so many kinds of whales and dolphins? BioScience 41(7):460-461. 9154

———, P. A. AKIN, AND J. V. KASHIWADA.

1991. Geographic variation in external morphology of the spinner dolphin *Stenella longirostris* in the eastern Pacific and implications for conservation. Fish. Bull., U.S. 89(3):411-428.. 9155

POLOVINA, J. J.

1991. Assessment of biological impacts of artificial reefs and FADs. *In* Indo-Pacific Fishery Commission (IPFC), Proceedings of the Symposium on Artificial Reefs and Fish Aggregating Devices as Tools for the Management and Enhancement of Marine Fishery Resources, Colombo, Sri Lanka, 14-17 May 1990, p. 258-263. Regional Office for Asia and the Pacific (RAPA), Food and Agriculture Organization of the United Nations, Bangkok. 9156

TABLE OF CONTENTS (CONTINUED)

———.
1991. A global perspective on artificial reefs and fish aggregating devices. *In* Indo-Pacific Fishery Commission (IPFC), Proceedings of the Symposium on Artificial Reefs and Fish Aggregating Devices as Tools for the Management and Enhancement of Marine Fishery Resources, Colombo, Sri Lanka, 14-17 May 1990, p. 251-257. Regional Office for Asia and the Pacific (RAPA), Food and Agriculture Organization of the United Nations, Bangkok. 9157

———.
1991. Evaluation of hatchery releases of juveniles to enhance rockfish stocks, with application to Pacific Ocean perch, *Sebastes alutus*. Fish. Bull., U.S. 89(1):129-136. 9158

———.
1991. Fisheries applications and biological impacts of artificial habitats. *In* W. Seaman, Jr. and L. M. Sprague (eds.), Artificial Habitats for Marine and Freshwater Fisheries, p. 153-176. Harcourt Brace Jovanovich, San Diego, California. 9159

RAMER, B. A., G. W. PAGE, AND M. M. YOKLAVICH.
1991. Seasonal abundance, habitat use, and diet of shorebirds in Elkhorn Slough, California. West. Birds 22(4):157-174. 9160

SAKAGAWA, G. T.
1991. Are U.S. regulations on tuna-dolphin fishing driving U.S. seiners to foreign-flag registry? N. Am. J. Fish. Mgmt. 11(3):241-252.. 9161

SCHWING, F. B., D. M. HUSBY, N. GARFIELD, AND D. TRACY.
1991. Mesoscale oceanic response to wind events off central California during spring 1989: analysis of CTD surveys and AVHRR imagery. Calif. Coop. Oceanic Fish. Invest. Rep. 32:47-62. 9162

SEKI, M. P., AND B. C. MUNDY.
1991. Some notes on the early life stages of the Pacific pomfret, *Brama japonica*, and other Bramidae from the central North Pacific Ocean. Jpn. J. Ichthyol. 38(1):63-68.. 9163

SHIMIZU, M., M. KUSAKARI, M. M. YOKLAVICH, G. W. BOEHLERT, AND J. YAMADA.
1991. Ultrastructure of the epidermis and digestive tract in *Sebastes* embryos, with special reference to the uptake of exogenous nutrients. Environ. Biol. Fishes 30:155-163.. 9164

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SMITH, M. K., AND E. KOSTLAN.
1991. Estimates of age and growth of ehu, *Etelis carbunculus*, in four regions of the Pacific from density of daily increments in otoliths. Fish. Bull., U.S. 89(3):461-471. 9165

SMITH, P. C., AND F. B. SCHWING.
1991. Mean circulation and variability on the eastern Canadian continental shelf. Cont. Shelf Res. 11(8-10):977-1012. 9166

SMITH, S. E., AND L. VLYMEN.
1991. Southwest Fisheries Science Center La Jolla Laboratory. *In* C. D. Becker (ed.), Fisheries Laboratories of North America, p. 149-151. Am. Fish. Soc., Bethesda, Maryland. 9167

SOMERTON, D. A.
1991. Detecting differences in fish diets. Fish. Bull., U.S. 89:167-169. 9168

———, AND D. R. KOBAYASHI.
1991. Bias in the Wetherall estimates of Z/K and L_∞ due to population disequilibria. Fishbyte 9(2):42-44. 9169

———, AND ———.
1991. Robustness of the Wetherall length-based method to population disequilibria. Fish. Bull., U.S. 89(2):307-314. 9170

SQUIRES, D., AND J. KIRKLEY.
1991. Production quota in multiproduct Pacific fisheries. J. Environ. Econ. Manage. 21:109-126. 9171

STEPIEN, C. A., AND R. H. ROSENBLATT.
1991. Patterns of gene flow and genetic divergence in the northeastern Pacific Clinidae (Teleostei: Blennioidei), based on allozyme and morphological data. Copeia 1991(4):873-896. 9172

SUDEKUM, A. E., J. D. PARRISH, R. L. RADTKE, AND S. RALSTON.
1991. Life history and ecology of large jacks in undisturbed, shallow, oceanic communities. Fish. Bull., U.S. 89:493-513. 9173

THOMSON, C. J.
1991. Effects of the avidity bias on survey estimates of fishing effort and economic value. Am. Fish. Soc. Symposium 12:356-366. 9174

WILLIAMS, A. B., AND R. B. MOFFITT.
1991. Crabs from the Mariana Archipelago: *Bothromaia griffini* new genus and species (Brachyura: Majidae), and remarks on *Poupinia hirsuta* Guinot (Homoloidea, Poupiniidae). Proc. Biol. Soc. Wash. 104(3):569-582. 9175

TABLE OF CONTENTS (CONTINUED)

WOODBURY, D., AND S. RALSTON.
1991. Interannual variation in growth rates and back-calculated birthdate distributions of pelagic juvenile rockfishes (*Sebastes* spp.) off the central California coast. Fish. Bull., U.S. 89(3):523-533. 9176

YOKLAVICH, M. M., AND G. W. BOEHLERT.
1991. Uptake and utilization of ^{14}C-glycine by *Sebastes melanops*. Environ. Biol. Fishes 30(1-2):147-153. 9177

———, G. M. CAILLIET, J. P. BARRY, D. A. AMBROSE, AND B. S. ANTRIM.
1991. Temporal and spatial patterns in abundance and diversity of fish assemblages in Elkhorn Slough, California. Estuaries 14(4):465-480. 9178

The following publications are not included in the Collected Reprints 1991:

ADAMS, P. B., AND W. M. SAMIERE.
1991. A computerized "expert system" to aid in the identification of juvenile rockfish (genus *Sebastes*). *In* T. E. Laidig and P. B. Adams (eds.), Methods used to identify pelagic juvenile rockfish (genus *Sebastes*) occurring along the coast of central California, p. 47-57. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-166.

———.
1991. Lingcod. *In* L. Low (ed.), Status of living marine resources off the Pacific coast of the United States as assessed in 1991, p. 16-17. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-210.

BALAZS, G. H., AND S. G. POOLEY (EDS.).
1991. Research plan for marine turtle fibropapilloma. Results of a December 1990 workshop. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-156, 113 p.

BENCE, J. R.
1991. Bocaccio. *In* L. Low (ed.), Status of living marine resources off the Pacific coast of the United States as assessed in 1991, p. 23-24. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-210.

BOEHLERT, G. W., AND J. YAMADA (EDS.).
1991. Rockfishes of the genus *Sebastes*: their reproduction and early life history. Environ. Biol. Fishes 30, Kluwer Academic Publishers, Dordrecht, 288 p.

TABLE OF CONTENTS (CONTINUED)

BOWLBY, C. E., P. D. SCOGGINS, R. T. WATSON, AND M. L. REDDY.
1991. Hawaiian monk seal, *Monachus schauinslandi*, at Kure Atoll, 1982-83. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-155, 29 p.

BRAHAM H. W., AND J. BARLOW (COMPILERS).
1991. Marine mammals. *In* L. Low (ed.), Status of living marine resources off the Pacific coast of the United States as assessed in 1991, p. 54-69. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-210.

BRILL, R. W., AND P. G. BUSHNELL.
1991. Effects of open- and closed-system temperature changes on blood oxygen dissociation curves of skipjack tuna, *Katsuwonus pelamis*, and yellowfin tuna, *Thunnus albacares*. Can. J. Zool. 69(7):1814-1821.

———, AND ———.
1991. Metabolic and cardiac scope of high energy demand teleosts, the tunas. Can. J. Zool. 69(7):2002-2009.

EDWARDS, E. F., AND P. M. KLEIBER.
1991. CHARTOPS: Simulating short-term use of the tuna purse-seine fleet to survey dolphin schools in the eastern tropical Pacific Ocean. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-163, 22 p.

HILL, P. S., A. JACKSON, AND T. GERRODETTE.
1991. Report of a marine mammal survey of the eastern tropical Pacific aboard the research vessel *McArthur*, July 28-December 6, 1990. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-159, 142 p.

———, R. C. RASMUSSEN, AND T. GERRODETTE.
1991. Report of a marine mammal survey of the eastern tropical Pacific aboard the research vessel *David Starr Jordan*, July 28-December 6, 1990. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-158, 133 p.

JACOBSON, L. D.
1991. Northern anchovy. *In* L. Low (ed.), Status of living marine resources off the Pacific coast of the United States as assessed in 1991, p. 40-42. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-210.

———.
1991. Thornyheads. *In* L. Low (ed.), Status of living marine resources off the Pacific coast of the United States as assessed in 1991, p. 29-30. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-210.

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LAIDIG, T. E., AND P. B. ADAMS (EDS.).
1991. Methods used to identify pelagic juvenile rockfish (genus *Sebastes*) occurring along the coast of central California. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-166, 180 p.

———, AND ———.
1991. Introduction: methods used to identify pelagic juvenile and larval rockfish (genus *Sebastes*) occurring along the coast of central California. *In* T. E. Laidig and P. B. Adams (eds.), Methods used to identify pelagic juvenile rockfish (genus *Sebastes*) occurring along the coast of central California, p. 1-5. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-166.

———, AND W. M. SAMIERE.
1991. Pigment patterns of juvenile *Sebastes flavidus* and *Sebastes melanops* useful in identification. *In* T. E. Laidig and P. B. Adams (eds.), Methods used to identify pelagic juvenile rockfish (genus *Sebastes*) occurring along the coast of central California, p. 7-18. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-166.

———, ———, AND R. C. DeFELICE.
1991. The use of the bones of the caudal complex to identify juvenile rockfish (*Sebastes* spp.). *In* T. E. Laidig and P. B. Adams (eds.), Methods used to identify pelagic juvenile rockfish (genus *Sebastes*) occurring along the coast of central California, p. 31-46. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-166.

MacCALL, A. D.
1991. Jack mackerel. *In* L. Low (ed.), Status of living marine resources off the Pacific coast of the United States as assessed in 1991, p. 43. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-210.

McBRIDE, A., AND J. E. HIGHTOWER.
1991. Predicting sablefish age using otolith characteristics. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-162, 19 p.

MORELAND, S. L., AND C. A. REILLY.
1991. Key to the juvenile rockfishes of central California. *In* T. E. Laidig and P. B. Adams (eds.), Methods used to identify pelagic juvenile and larval rockfish (genus *Sebastes*) occurring along the coast of central California, p. 59-180. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-166.

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OLIVER, C. W., AND R. L. BUTLER.
1991. Documentation of the 1980 data verification programs and common subroutines for fixed-format data: porpoise data management system. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-157, 69 p.

PEARSON, D. E.
1991. Chilipepper. *In* L. Low (ed.), Status of living marine resources off the Pacific coast of the United States as assessed in 1991, p. 27-28. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-210.

———.
1991. Shortbelly rockfish. *In* L. Low (ed.), Status of living marine resources off the Pacific coast of the United States as assessed in 1991, p. 20. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-210.

———.
1991. Yellowtail rockfish. *In* L. Low (ed.), Status of living marine resources off the Pacific coast of the United States as assessed in 1991, p. 31-32. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-210.

———, AND J. E. HIGHTOWER.
1991. Spatial and temporal variability in growth of widow rockfish (*Sebastes entomelas*). U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-167, 43 p.

———, AND ———.
1991. Canary rockfish. *In* L. Low (ed.), Status of living marine resources off the Pacific coast of the United States as assessed in 1991, p. 25-26. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-210.

———, AND ———.
1991. Widow rockfish *In* L. Low (ed.), Status of living marine resources off the Pacific coast of the United States as assessed in 1991, p. 21-22. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-210.

PHILBRICK, V., P. FIEDLER, S. REILLY, R. PITMAN, L. BALLANCE, G. THOMAS, AND D. BEHRINGER.
1991. Report of ecosystem studies conducted during the 1990 eastern tropical Pacific dolphin survey on the research vessel *David Starr Jordan*. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-160, 117 p.

TABLE OF CONTENTS (CONTINUED)

———, ———, ———, ———, ———, ———, AND ———.
1991. Report of ecosystem studies conducted during the 1990 eastern tropical Pacific dolphin survey on the research vessel *McArthur*. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-161, 123 p.

RALSTON, S. V.
1991. Other rockfish. *In* L. Low (ed.), Status of living marine resources off the Pacific coast of the United States as assessed in 1991, p. 33-34. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-210.

SCHWING, F. B., S. RALSTON, D. M. HUSBY, AND W. H. LENARZ.
1991. The nearshore physical oceanography off the central California coast during May-June 1989: a summary of CTD data from juvenile rockfish surveys. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-153, 123 p.

SILBERBERG, K. R.
1991. Identification of juvenile rockfish (genus *Sebastes*) using the cleithrum. *In* T. E. Laidig and P. B. Adams (eds.), Methods used to identify pelagic juvenile and larval rockfish (genus *Sebastes*) occurring along the coast of central California, p. 19-30. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-166.

STAFF OF THE SOUTHWEST FISHERIES SCIENCE CENTER.
1991. Status of Pacific oceanic living marine resources of interest to the USA for 1991. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-165, 78 p.

THOMSON, C. J., AND S. J. CROOKE.
1991. Results of the southern California sportfish economic survey. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-164, 264 p.

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Session V

REPRODUCTIVE SUCCESS OF SPRAT (*SPRATTUS SPRATTUS*) IN GERMAN BIGHT DURING 1987

by

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ABSTRACT

The SARP "within year" experiment was carried out on sprat by Alshuth (1988a) in the German Bight in 1987 when production of small larvae was determined over the entire spawning season from April to August and, subsequently, the birth-date distribution of the juveniles which were surviving until November was established.

These data were now analysed in relation to wind speed, stability of the water column and tidal impact. The ratios of the birth-date frequencies, found by counting daily otolith marks, to the within-season variations of larval production indicate only modest survival during late May and early June even though substantial larval production was indicated. However, a period of consistently low wind conditions occurred from June 9 to June 27. Correspondingly, the apparent survival rate during the final two weeks of June increased several fold over that of the preceeding four weeks. However, during the first half of July following a period of higher winds from 29 June to 4 July the apparent survival rate declined somewhat. In late July and early August the apparent survival rate again increased to the highest values found during the operation, even though some wind events of lesser intensity than the early July event occurred during the period.

INTRODUCTION

Methot (1983) introduced an elegant method when studying recruitment variability of the northern anchovy, ***Engraulis ringens***, in the California Current, a species with a protracted spawning season of about seven months. He recorded the production of young anchovy larvae over the entire spawning period from December to June of the following year. Subsequently, he collected the juveniles several months after spawning season and determined their birthdate distribution by counting daily rings on their otoliths. The birthdate distribution curve of the juveniles was then compared to the larval production curve to identify periods of heavy mortality or of exceptional survival of different cohorts of larvae. These "exceptional" periods can then be matched with environmental data sets to determine the causes of heavy mortality or good survival.

So, by analyzing larval production, birthdate distribution of juveniles and oceanographic, meteorological observations one can record intra-seasonal changes in larval survival, pinpoint critical periods of survival and identify the causal mechanisms.

This high temporal resolution experiment was refined by the Southwest Fisheries Center under the leadership of Reuben Lasker (Lasker 1985) and became known as the "within-year exercise" in SARP studies (Bakun et al. 1991). It has been identified as a uniquely promising process-oriented approach for analyzing the causal mechanisms and consequences of short-term larval survival (Anon. 1983, 1984, 1987). The particular advantage of this approach is that it addresses the problem on the population level, rather than addressing the fate of typical or "average" larvae which may be irrelevant to net reproductive success (Bakun et al. 1991).

As larval production can vary on small temporal scales, frequent surveys are required to establish a valid larval production curve. Because of the high demand of ship time and other operational resources required, no fully elaborated SARP "within-year" exercise , incorporating a full suite of environmental and biological data, has been completed to date (Bakun et al. 1991).

A first attempt to apply the "within-year" experiment to North Sea sprat, ***Sprattus sprattus***, was made in the German Bight in 1987 (Alshuth 1988a, 1988b). Larval production of sprat in the German Bight was monitored and the birthdate distribution of the juveniles was established subsequently. However, no analysis of causal mechanims of the differential "within-season" larval mortality was done. The objective of this study is to relate the results of Alshuth's studies (1988a) to wind speed, tidal impact and stability of the water column.

LARVAL PRODUCTION AND BIRTHDATE DISTRIBUTION OF JUVENILES

Larval production was determined by eight fortnightly cruises over the entire spawning season from the second half of April to the first half of August on a grid of 14 sampling stations spread evenly over the German Bight (Fig. 1). The larvae were collected by oblique bongo tows and only larvae up to 5 mm length were considered for the production estimate (Alshuth 1988a). Juveniles were collected in October and November with a RMT and their age was determined subsequently by counting daily rings on the otoliths (Alshuth 1988a). A comparison of the birthdate distribution of the juveniles and the larval production curve clearly indicates differential "within-season" mortality of the different larval cohorts (Fig. 2). The almost identical birthdate distribution of juveniles caught in mid-October and those caught four weeks after that shows that there was no differential mortality during this juvenile phase.

DISCUSSION

This initial SARP field study of sprat in the German Bight was more a "proof of concept" for the development of a short-time scale "survival index" than a complete SARP "within-year" exercise. That is, it did not include a comprehensive suite of equally high frequency measurements of the physical and biological environment, histological measures of starvation (Theilacker 1986), immunoassays of predator stomach contents (Theilacker et al. 1986), etc. Thus, the data available for interpretation of the indicated short time-scale variations is minimal. Stability of the water column, tidal impact and local wind conditions were analyzed in relation to the survival index of the juveniles.

Analysis of the tidal regime and the stability of the water column did not indicate any relationship with the survival index. However, variability in local wind conditions showed interesting relationships to the differential survival index of sprat juveniles in the German Bight.

Wind effects are involved in many of the currently popular hypotheses concerning regulation of recruitment variability. Nutrient enrichment of the illuminated upper zone of the ocean by wind-driven upwelling or mixing may be important in maintaining the trophic base for production of larval food. A wind-based index of coastal upwelling (Bakun 1973) has been empirically related to population dynamics of a number of commercial fish stocks of the California Current and other eastern ocean upwelling systems (Bakun and Parrish 1981, Shepard et al. 1984, Bakun 1985, Bakun in press). The hypothesis of Lasker (1975, 1978, 1988), which addresses detrimental effects of dispersion of fine scale food particle strata by wind-induced turbulent mixing, has been very influential in the development of SARP. Lasker's hypothesis is supported by the analysis of Peterman and Bradford (1987), who empirically related interyear variability in larval anchovy mortality rate off California to frequency of calm periods of sufficient duration for fine scale strata of food organisms to form. Rothchild and Osborn (1988) have suggested that certain levels of turbulence could actually enhance feeding efficiency of small marine organisms. Parrish et al. (1981) surveyed reproductive habits of fishes of the California Current and found a pattern of avoidance of detrimental effects of wind-induced offshore Ekman transport , which would carry eggs and larvae away from the favourable coastal habitat. Identification of similar patterns in other types of fish stocks and regional settings, indicating wide-spread importance of "physical retention areas", have lead to Sinclair's (1988) formulation of the "member/vagrant" hypothesis. Parrish et al. (1983) show a pervasive tendency, in reproductive habits of eastern ocean coastal pelagic fishes, for simultaneous minimization of exposure of larvae to both offshore transport and turbulence. Cury and Roy (1989) have used new non-linear methods (Mendelssohn and Cury 1987), to empirically demonstrate a consistent "optimal environmental window", where reproductive success is favoured at an intermediate range of wind speed, neither too low for adequate upwelling-based enrichment nor so high that excessive offshore transport and turbulent mixing occurs. Roy (1990) showed the same pattern of apparent selection for an intermediate ideal characteristic wind speed in a survey of the reproductive habits of West African coastal pelagic fishes.

Indices of wind-related processes

Several series of wind-related indices (Fig. 3 A, B, C) related to the various hypotheses enumerated above, have been prepared. The basic data source is the file of 6-hourly northern hemisphere synoptic atmospheric pressure/wind analyses produced at the U.S.Navy's Fleet Numerical Oceanography Center in Monterey, California. From these a series of estimates of the local surface wind in the German Bight was produced according to the method of Bakun (1973). The "wind mixing index" (Fig. 3A) is an estimate of the rate of transfer of wind-derived turbulent mixing energy through the sea surface; it is formed as the bi-weekly average of the third power (cube) of the wind speed (Bakun and Parrish 1980).

In addressing Lasker's hypothesis, it is probably not the average mixing intensity that is crucial, but the existence of adequate temporal "windows" (Bakun and Parrish 1980) during which the production of turbulent mixing energy remains low for a long enough period for concentrated food particle strata to accumulate and for larvae to accomplish successful "first-feeding". These calm periods have been called variously "Lasker events", "Lasker gates", etc. Here we specify a "Lasker (x,y) window" as being a full day in which the wind speed did not exceed "x" m s $^{s-1}$, which directly follows an unbroken sequence of at least "y" preceeding days with wind speeds not exceeding the same "x" m^{-1} limit. Peterman and Bradford (1987) chose 10 m s^{-1} for the wind speed limit for their study of California anchovy. Mendelssohn and Mendo (1987) chose 5 m s^{-1} for their study of Peruvian anchovy. We show both (5,4) and (10,4) Lasker windows for the period and location of the 1987 German Bight "Sprat-SARP" operation in Fig. 3 .

The stress exerted by the wind on the sea surface was computed from the synoptic surface wind estimates using the standard quadratic drag law and assuming a constant drag coefficient of 0.0013. The resulting stress estimates where then averaged by component for each bi-weekly increment of the study (e.g., Fig. 3C).

The survival index (Fig. 3D) was defined as the ratio of the percentage of the sampled larval birthdates (Fig. 2A) in each bi-weekly increment to the corresponding larval production estimates (Fig. 2A and Fig. 3E). The survival index (Fig. 3D) was defined as the ratio of the percentage of the sampled larval birthdates (Fig. 2) in each biweekly increment to the corresponding larval production estimates (Fig. 2 and Fig. 3E).

We can examine these series for apparent conformities to the hypothetical linkages. However, lacking corroborating data on sub-surface processes and effects, the analysis is at this point merely correlative and subject to all well-known limitations of a correlative approach (e.g. Bakun 1985). Note also that the period of substantial larval production contains only five bi-weekly increments (Fig. 3E) with perhaps two other data points (first half of May and first half of August) having very uncertain relative magnitude of survival because of very low indicated larval production but at least an indication that survival may have been rather good. Accordingly, the degrees of freedom available for any sort of empirical analysis are extremely limited. Thus the brief analysis that follows should be properly regarded as merely an exercise in hypothesis generation. No implication that this dis-cussion in any way constitutes a valid hypothesis test is intended.

Larval retention hypothesis

The most evident visual correlation appears to be with eastwards wind stress (Fig. 3C). The orthogonal northward component showed no perceptabel degree of correlation. Eastwards stress would produce southward surface Ekman transport (Ekman 1905) in a deep ocean situation. However, in a shallow area such as the coastward portions of the German Bight, frictional effects would probably cause the transport to be angled somewhat more directly downwind than the "90° to the right" specified by the "pure" Ekman transport derivation. Thus, the near surface transport from an eastward wind stress would, in all likelihood, be directed from the North Sea at large, directly into the German Bight. This would tend to hold drifting larvae within the shallow portions of the German Bight, retarding their dispersion into the open North Sea, and helping to keep them as "members" rather than becoming "vagrants", according to the terminology of Sinclair (1988). In the shallower parts of the German Bight, larvae may find improved feeding conditions within the frontal systems produced by the fresh water inflows and perhaps find some refuge from predation, etc. In addition, since the birthdate distributions which deter-mine the survival index are collected locally, the variation of the proportion of "members" to "vagrants" may be of comparable significance to variations in actual survival in determining the variability of the survival index.

Stable ocean hypothesis (Lasker's hypothesis)

The most notable deviation from a direct visual proportionality of survival index (Fig. 3D) to eastward wind stress (Fig. 3C) is a period of relatively enhanced apparent survival during the second half of June. This period corresponds to a period of consistently low winds yielding eleven Lasker (5,4) windows within the 15-day period (dark shading Fig. 3B). We note that the spawning period of sprat (Fig. 3E) is confined to the seasonal period of low turbulent mixing energy production by the wind (Fig. 3A). The one two-week period where an indication of substantial survival (Fig. 3D) corresponds to a period of relatively high mixing index (Fig. 3A) is during the first half of May where presence of four "Lasker (4,5) windows" indicates an extended period of calm conditions even although the mean turbulence generation, for the period as a whole, was high.

SUMMARY

Thus, looking only at potential wind effects, the results of the 1987 German Bight Sprat-SARP exercise appear to be consistent with a combination of favourable effects of (i) larval retention (Parrish et al. 1981; Sinclair 1988) and of (ii) water column stability during early larval life (Lasker 1975, 1978). There is little evidence here for any substantial favourable effect of increased turbulence generation, acting either to stimulate food particle production by mixing nutrients from the pycnocline into the upper mixed layer or to increase contact rates (Rothchild and Osborn 1988) between feeding larvae and appropriate food particles.

REFERENCES

Anon. 1983. Workshop on the IREP Component of the IOC Programme on Ocean Science in Relation to Living Resources (OSLR). IOC Workshop Rep. No. 33. Intergovernmental Oceanographic Commission, Unesco, Paris. 51pp.

Anon. 1984. IOC-FAO Guiding Group of Experts on the Programme of Ocean Sciencwe in Relation to Living Resources, First Session. Reports of Meetings of Experts and Equivalent Bodies SC-84/WS/18. Intergovernmental Oceanographic Commission, Unesco, Paris. 34pp.

Anon. 1987. IOC-FAO Guiding Group of Experts on the Programme of Ocean Sciencwe in Relation to Living Resources, Second Session. Reports of Meetings of Experts and Equivalent Bodies SC-87/WS/41. Intergovernmental Oceanographic Commission, Unesco, Paris. 37pp.

Alshuth, S. 1988a. Bestimmung von Alter und Wachstumsraten bei Larven und Juvenilen der Sprotte, *Sprattus sprattus* L.. Ph. D. Thesis, Universität Bremen. 191pp.

Alshuth, S. 1988b. Seasonal variations in length-frequency and birthdate distribution of juvenile sprat (*Sprattut sprattus* L.). ICES C.M. 1988./H:44, 12pp.

Bakun, A. (in press). The California Current, Benguela Current, and Southwestern Atlantic Shelf Ecosystems: A comparative approach to identifying factors regulating biomass yields. *In* Large Marine Ecosystems. K.Sherman, L.M.Alexander, and B.Gold (eds.) American Association for the Advancement of Science.

Bakun, A. 1973. Coastal upwelling indices, west coast of North America, 1946-71. NOAA Tech. Rep. NMFS SSRF-671, 103 pp.

Bakun, A. 1990. Global climate change and intensification of coastal ocean upwelling. Science 247: 198-201.

Bakun, A and R.H. Parrish. 1980. Environmental inputs to fishery population models for eastern boundary current regions. pp. 67-104. In: G.D. Sharp (ed) Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes, Lima, Peru, 20 Apr.-5 May, 1980. IOC Workshop Rep. 28: 323 pp.

Bakun, A., J. Alheit and G. Kullenberg. 1991. The Sardine-Anchovy Recruitment Project (SARP): rationale, design and development. ICES C.M. 1991/L:43, 16pp.

Cury, P. and C. Roy. 1989. Optimal window and pelagic fish recruitment success in upwelling areas. Can J. Fish. Aquat. Sci. 46: 670-680.

Ekman, V.W. 1905. On the influence of the earth's rotation on ocean currents. Ark. Mat. Astron. Fys. 2(11): 1-55. (reprinted in J. Cons. int. Explor. Me 20(2), 1954).

Lasker, R. 1975. Field criteria for survival of anchovy larvae: the relation betwen inshore chlorophyll maximum layers and successful first feeding. Fish. Bull. U.S. 73: 453-462.

Lasker, R. 1978. The relation between oceanographic conditions and larval anchovy food in the California Current: Identification of the factors leading to recruitment failure. Rapp. P.-v. Reun. Cons. int. Explor. Mer. 173: 212-230.

Lasker, R. 1985. What limits clupeoid production? Can. J. Fish. Aquat. Sci. 42: 31-38.

Lasker, R. 1988. Studies on the northern anchovy: biology, recruitment, and fishery oceanography. pp. 24-41. *In* Studies on Fisheries Oceanography. Proceedings of the 25th Anniversary Symposium "Fisheries and Fishery Oceanography in the Coming Century". Tokyo, 10-13 November, 1986. Japanese Society of Fishery Oceanography.

Mendelssohn, R. and P. Cury. 1987. Fluctuations of a fortnightly abundance index of the Ivorian coastal pelagic species and associated environmental conditions. Can. J. Aquat. Sci. 44: 408-421.

Mendelssohn, R. and J. Mendo. 1987. Exploratory analysis of anchoveta recruitment off Peru and related environmental series. p. 294-306. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian Anchoveta and its Upwelling Ecosystem: Three Decades of Change. ICLARM Studies and reviews 15. Instituto del Mar del Peru, (IMARPE), Callao, Peru; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines, 351 pp.

Methot, R.D. 1983. Seasonal variation in survival of larval *Engraulis mordax* estimated from the age distribution of juveniles. Fish. Bull., U.S. 81: 741-750.

Parrish, R.H., A. Bakun, D.M. Husby and C.S. Nelson. 1983. Comparative climatology of selected environmental processes in relation to eastrern boundary current pelagic fish reproduction. *In* Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources. pp. 731-778. Ed. by G.D. Sharp and J. Csirke. FAO Fish. Rep. 291: 1224 pp.

Parrish, R.H., C.S. Nelson and A. Bakun. 1981. Transport mechanisms and reproductive success of fishes in the California Current. Biol. Oceanogr. 1: 175-203.

Peterman, R.M. and M.J. Bradford. 1987. Wind speed and mortality rate of a marine fish, the northern anchovy (*Engraulis mordax*). Science 235: 354-356.

Rothchild, B.J. and T.R. Osborn. 1988. Small-scale turbulence and plankton contact rates. J. Plankton Res. 10: 465-474.

Roy, C. 1990. Réponses des stocks de poissons pélagiques á la dynamique des upwellings en Afrique de l'Ouest: analyse et modèlisation. Thèse de Doctorat. Universitè de Bretagne Occidental, Brest, France. 147 pp.

Shepard, J.G., J.G. Pope and R.D. Cousins. 1984. Variations in fish stocks and hypotheses concerning their links with climate. Rapp.P.-v. Reun. Cons. int. Explor. Mer 185: 255-267.

Sinclair, M. 1988. Marine Populations: an essay on population regulation and speciation. University of Washington Sea Grant Program (Distributed by University of Washington Press. Seattle and London.). 252 pp.

Theilacker, G.H. 1986. Starvation-induced mortality of young sea-caught jack mackerel, *Trachurus symetricus*, determined with histological and morphological methods. Fish. Bull., U.S. 84: 1-17.

Theilacker, G.H., A.S. Kimball and J.S. Trimmer. 1986. Use of ELISPOT immunoassay to detect euphausid predation on larval anchovy. Mar. Ecol. Progr. Ser. 30: 127-131.

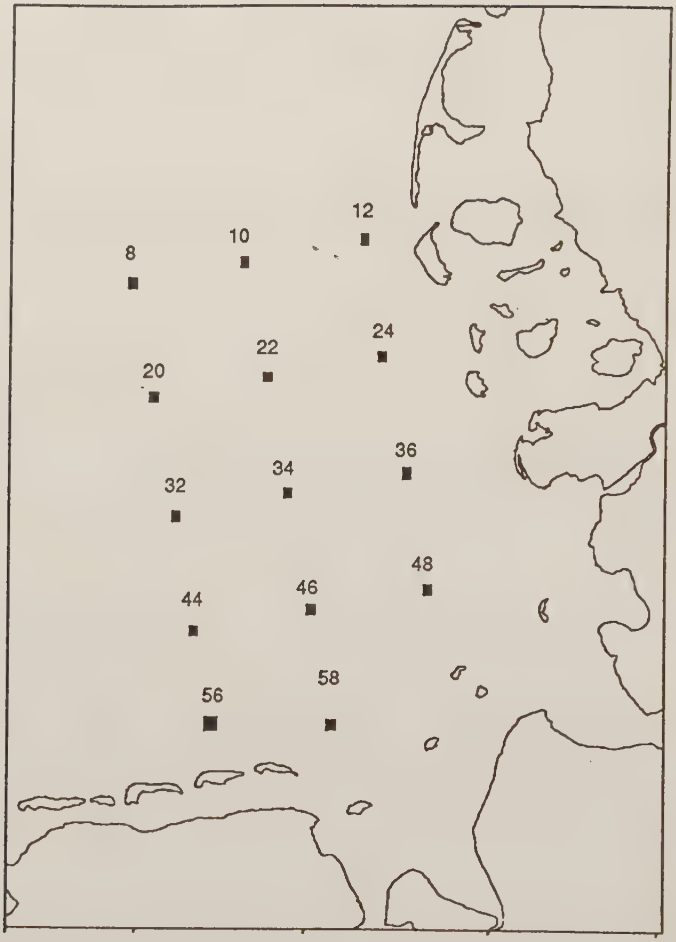
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Fig. 1: Study area in German Bight with location of sampling stations.

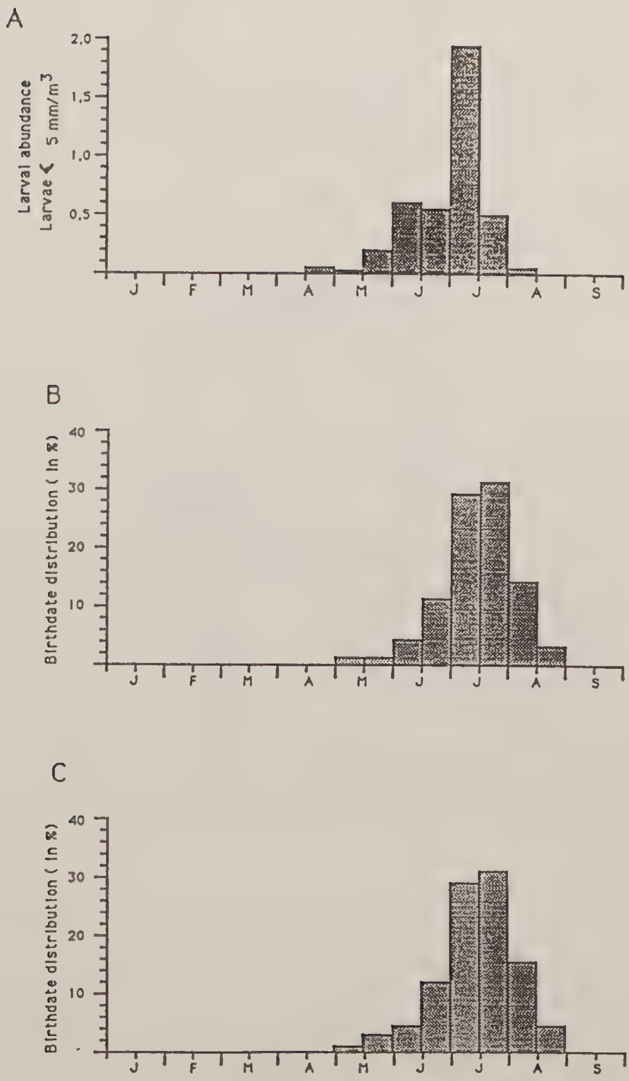

Fig. 2: A - Seasonal distribution of abundance of larval sprat in German Bight in 1987.

B - Seasonal distribution of birthdates of juvenile sprat collected 13/14 October 1987 in German Bight

C - Seasonal distribution of birthdates of juvenile sprat collected 11 November in German Bight

(modified after Alshuth 1988 a,b)

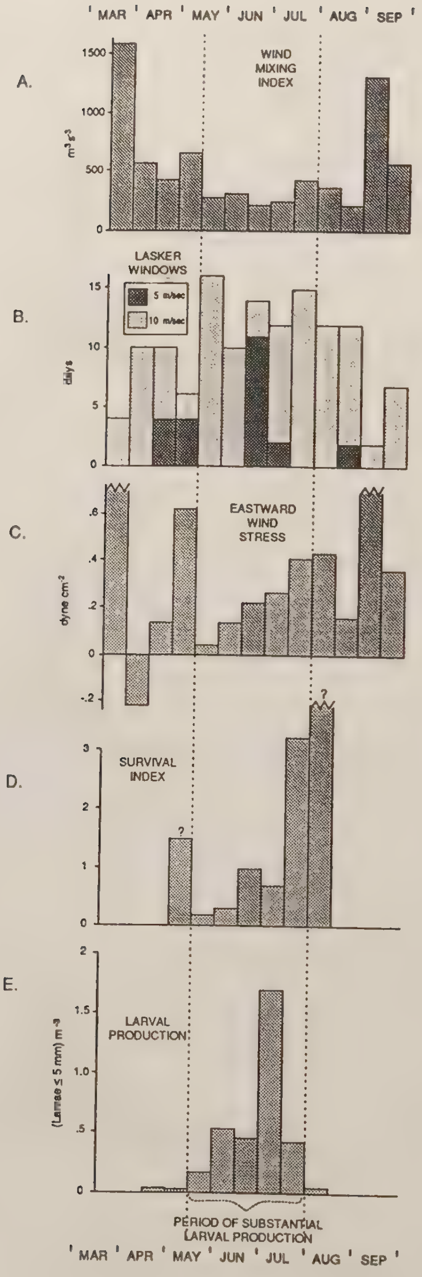

Fig. 3: A, B, C - Series of wind-related indices.

D - Survival Index of juvenile sprat.

E - Larval production of sprat (as Fig. 2 A).

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México

ABUNDANCIA Y DISTRIBUCION BATIMETRICA DIURNA Y NOCTURNA DE LOS SIFONOFOROS DURANTE LAS CUATRO ESTACIONES DEL AÑO 1969, EN AGUAS DE CALIFORNIA Y BAJA CALIFORNIA

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RESUMEN

Las colecciones de plancton se obtuvieron con redes bongo de apertura y cierre automáticos, día y noche en la misma localidad en ocho estratos desde 0 hasta 600 m de profundidad. Se determinaron sesenta y ocho especies en estas colecciones. Se incluye el estudio de cuarenta y nueve especies, ya que las especies *Chelophyes appendiculata, Muggiaea atlantica* y *Eudoxoides spiralis* se analizaron en Alvariño (1980; Proc. 4th Int. Coelenterates Conf., Sep. 1979; Interlaken, Switzerland), y dieciseis especies del género *Lensia* en Alvariño (1985; Inv. Mar. CICIMAR 2(1)). En general se ha observado que la mayor parte de las especies habitaban niveles más profundos de día que de noche. Asimismo, las poblaciones de eudoxias habitaban estratos más profundos que las de la fase poligástrica. Las épocas de reproducción de la mayor parte de las especies están bien definidas. Se determina las especies que habitan los niveles de las zonas epipelágica y mesopelágica, aunque algunas especies de sifonóforos recorren en sus desplazamientos estratos amplios de las zonas epi-, meso- y batipelágicas. La tabla detalla para cada especie la abundancia, en relación con la fecha, hora y profundidad del arrastre para cada estación del año y localidad. Para cada estación se incluyen mapas con la distribución de las Estaciones y los perfiles para cada enfilación de Estaciones, donde se indican los estratos correspondientes a los arrastres de plancton.

ABSTRACT

The plankton collections were obtained with bongo nets of automatic open-clossing devices. The tows were made day and night at the same locations at eight bathymetric levels, from 0 to 600 m deep, during the four seasons of 1969. Sixty eight species of Siphonophora were obtained in these regions. This work includes only forty nine species, because the study of *Chelophyes appendiculata, Muggiaea atlantica* and *Eudoxoides spiralis* were published in Alvariño (1980; Proc. 4th Int. Coelenterates Conf., Sep. 1979; Interlaken, Switzerland), and sixteen species of the genus *Lensia* in Alvariño (1985; Inv. Mar. CICIMAR 2(1)). In general, it was observed that most of the species inhabit deeper levels during daylight than at night, also, the eudoxia populations inhabited deeper strata than the polygastric populations. However, some siphonophores are able to swimm throughout wide bathymetric strata, from the epi-, meso- and bathypelagic zones. A table includes in detail for each species, abundance related to date, time and depth of the haul for each location and season. Maps with the distribution of the Stations, and profiles for each line of Stations showing the levels at which plankton hauls were obtained are included for each season.

INTRODUCCION

La distribución de los sifonóforos en aguas de California y Baja California es conocida por el trabajo de Alvariño (1971) en donde se discute la distribución de las especies en todos los océanos y las zonas batimétricas que habitan, recopilando también toda la información publicada hasta entonces. En Alvariño (1971) se incluyen los resultados obtenidos con el estudio de las colecciones procedentes de dieciseis expediciones en el Océano Pacífico y otras expediciones en el Atlántico e Indico, y además se analizan las colecciones procedentes de los cruceros mensuales de CalCOFI frente a California y Baja California durante 1954 (enero-diciembre), 1956 (febrero-abril), 1958 (enero-octubre), 1959 (enero), 1961 (enero), 1965 (agosto). En ese trabajo se presenta además una tabla con la distribución geográfica y con la distribución batimétrica de las especies.

Barham (1963, 1966) estudió en aguas de California las migraciones de algunos sifonóforos en el estrato de dispersión. Bigelow y Leslie (1930) analizaron los sifonóforos de Monterey (California) en donde señalaban la presencia de *Muggiaea atlantica* (*Sphaeronectes truncata*), *Lensia conoidea* (*Diphyes truncata*), *Chuniphyes multidentata, Vogtia pentacantha, V. spinosa, Nectodroma reticulata*.

Alvariño (1967a) describe una nueva especie de *Vogtia* (*V. kuruae*) en aguas de California, en 1972 se captura en California un ejemplar de *Epibulia ritteriana* que se describe en Alvariño (1972), y en Alvariño (1983a) esta autora describe un nuevo género y especie de *Prayinae* (*Nectocarmen antonioi*) que se obtuvo en colecciones procedentes de California.

Alvariño (1967b) realizó un estudio sobre la distribución batimétrica de los sifonóforos frente a San Diego, California. En este estudio se obtuvieron treinta especies en las colecciones diurnas y nocturnas; aunque se observó el mismo número de especies, muchas de ellas no eran comunes a los arrastres diurnos y nocturnos. Así, *Clausophyes ovata, Lensia challengeri, L. hotspur, L. subtilis, Stephanomia rubra, Physophora hydrostatica* no se observaron en las colecciones nocturnas, y *Ceratocymba dentata, Lensia ajax, L. grimaldii, L. hostile, Amphicaryon ernesti, Nectopyramis diomedeae, N. thetis, Archisoma natans* no se observaron en las colecciones diurnas.

Pugh (1974, 1977) se ha ocupado las variaciones en la distribución batimétrica de los sifonóforos en las aguas cálidas del Atlántico.

Un total de cincuenta y ocho especies de sifonóforos se determinaron en Alvariño (1971) en aguas de California y Baja California.

Bigelow (1911) publicó un excelente trabajo sobre los sifonóforos del Pacífico tropical oriental, que ha servido de base para todos los investigadores interesados en estos Celentércos.

Alvariño (1969) determinó dieciocho especies de Sifonóforos en el Mar de Cortés. Alvariño (1972b) estudió los sifonóforos de la zona del Pacífico frente a la América Central y México, y en Alvariño (1974) se ocupó de los sifonóforos de la zona del Canal de Panamá.

El estudio de las colecciones diurnas y nocturnas obtenidas en las cuatro estaciones del año 1969 frente a California y Baja California, dieron como resultado la existencia de sesenta y ocho especies en estas aguas.

En los estudios sobre sifonóforos no se ha observado estrecha relación entre las condiciones hidrográficas y la distribución de las especies. Sin embargo, Alvariño (1971) señala la importancia de la isoterma a 200 m de profundidad, y discute la distribución de las especies en relación con dicha isoterma, presentando en los mapas esos factores. Los perfiles de temperatura, salinidad y oxígeno correspondientes a las tres enfilaciones de estaciones en aguas de California y Baja California, incluyendo los datos obtenidos durante los cruceros que han recolectado las muestras de plancton que aquí se estudiaron, correspondientes a las cuatro estaciones del año 1969, están publicados en Alvariño (1983a).

Actualmente están en progreso estudios sobre las relaciones entre la distribución de las especies de Sifonóforos y otros zooplanctontes, y las características hidrográficas y otros factores ambientales, en aguas de California y Baja California.

MATERIAL Y METODOS

En la serie de cruceros que durante 1969 exploraron las regiones de California (E.E.U.U.) y Baja California (México), se han obtenido muestras de plancton durante las cuatro estaciones de ese año en localidades distribuidas a lo largo de los perfiles 70, 90 y 120 de CalCOFI. En cada crucero se efectuaron series de arrastres batimétricos en once localidades distribuidas en las tres enfilaciones mencionadas. Las estaciones son: 70.60, 70.75, 70.90, 70.110, 90.45, 90.60, 90.90, 120.45, 120.55, 120.70, 120.90.

El crucero de invierno correspondía a febrero y marzo (6902-03), el de primavera a mayo y junio (6905-06), el de verano comprendía agosto y septiembre (6908-09) y el de otoño a noviembre y diciembre (6911-12).

El crucero de invierno (6902-03) ha sido de prueba de técnicas de muestreo y equipos, y durante el mismo, los arrastres alcanzaron niveles batimétricos variables, y las redes nunca rebasaron los 300 m de profundidad.

Las muestras de plancton se obtuvieron día y noche en cada localidad y estratos batimétricos, aproximadamente a mediodía y medianoche. Los arrastres se efectuaron a niveles de 25 m en los 100 m de los estratos epipelágicos (25-0, 50-25, 75-50, 100-75), y cada 125 m desde los 100 m hasta los 600 m (profundidad máxima alcanzada por los arrastres) abarcando los estratos 225-100, 350-225, 475-350, 600-475 m.

Se emplearon redes bongo de apertura y cierre automáticos. La apertura de malla de las redes era de 505 micras y 333 micras y los copos respectivamente de 333 micras y 223 micras.

Los flujómetros acoplados a las redes efectuaban el cierre de las mismas cuando el volumen del agua filtrada por las dos redes del par en cada estrato batimétrico alcanzaba 1000 m^3. En los arrastres que abarcaban los estratos de 25 m se filtraban 40 m^3 de agua por cada metro de profundidad, en cambio, en los estratos que abarcaban 125 m se filtraban 8 m^3 de agua por cada metro de estrato. Para computar los datos obtenidos hay que normalizar la cantidad de agua filtrada por cada metro de arrastre en los estratos de 25 m y 125 m ya que las redes en los estratos de 125 m efectuan arrastres a mayor velocidad (5 veces mayor) que en los estratos de 25 m. Esta diferencia de velocidad de arrastre constituye un importante problema que afecta a la captura de los organismos planctónicos. Por lo tanto, para normalizar los datos numéricos por encima y por debajo de los 100 m de profundidad, se multiplican por 5 los correspondientes a los estratos de 125 m.

La fórmula que se aplica es:

N = n · (Prof. de apertura - Prof. de cierre)/25

Detalles sobre esta fórmula y demás datos sobre métodos se encuentran en Alvariño (1985) y Alvariño *et al.* (1990).

Los ejemplares de sifonóforos se identificaron y contaron para cada una de las especies obtenidas en la muestra total. No se obtuvieron alícuotas. Si una red del par no ha cerrado, se estimó que contenía el mismo número de ejemplares que la otra red del par. La información que se incluye corresponde únicamente a las muestras obtenidas en los arrastres en los que al menos una red funcionó adecuadamente. Si un arrastre no se efectuó, o si ambas redes no funcionaron bien, no existe forma de interpolar los valores para las especies y número de individuos por especie que se encontraban en aquella localidad, profundidad, fecha y hora.

Existen dificultades para cuantificar el número de ejemplares para cada especie de sifonóforos. En el caso de las familias Diphydae, Clausophyidae y Abylidae, se determinaron las fases poligástricas y de eudoxia. El valor numérico de individuos para cada una de estas fases corresponde al número más elevado que se ha obtenido en la muestra, ya sea del nectóforo superior o inferior (fase poligástrica), y la bráctea o el gonóforo (fase eudoxia). En el caso de especies de otras familias de Calycophorae se emplean otros métodos. Así, en los Prayidae e Hippopodiidae los nectóforos y las brácteas indicarán la presencia de la especie, y solamente el número de pneumatóforos indicará para los Cystonectae y Physonectae la cantidad de animales y asimismo en este caso los nectóforos y brácteas señalan la presencia de la especie (Alvariño, 1985; Alvariño *et al.*, 1990).

Se incluye una tabla con la abundancia de individuos para cada especie de Siphonophora, en cada estación del año, localidad, profundidad, fecha y hora. Además, cuando es pertinente se indica la abundancia de las fases poligástricas y de eudoxia o fase de reproducción.

RESULTADOS

Durante los cruceros realizados en las cuatro estaciones de 1969, se determinaron sesenta y ocho especies de Sifonóforos, dis-

Sub-orden CYSTONECTAE

Familia Epibulidae: *Epibulia ritteriana* Haeckel, 1888.

Sub-orden PHYSONECTAE

Familia Apolemiidae: *Apolemia uvaria* (Lesueur, 1811).

Familia Agalmidae: *Agalma okeni* Eschscholtz, 1825.

A. elegans (Sars, 1836).

Stephanomia bijuga (delle Chiaje, 1841-1842).

S. rubra Vogt, 1825.

Erenna richardi Bedot, 1904.

Nanomia cara A. Agassiz, 1865.

Moseria convoluta (Moser, 1925).

Familia Pyrostephidae: *Bargmannia elongata* Totton, 1954.

Familia Physophoridae: *Physophora hydrostatica* Forskål, 1775.

Familia Athorybiidae: *Athorybia rosacea* (Forskål, 1775).

Familia Forskaliidae: *Forskalia edwardsi* Kölliker, 1853.

Sub-orden CALYCOPHORAE

Familia Prayidae

Sub-familia Amphicaryoninae: *Amphicaryon acaule* Chun, 1888.

A. ernesti Totton, 1954.

Sub-familia Prayinae: *Rosacea plicata* Quoy & Gaimard, 1827.

R. cymbiformis (delle Chiaje, 1822).

Nectodroma dubia (Quoy & Gaimard, (1833, 1834).

N. reticulata (Bigelow, 1911).

Desmophyes annectens Haeckel, 1888.

Nectocarmen antonioi Alvariño, 1983.

Sub-familia Nectophyramidinae: *Nectopyramis diomedeae* Bigelow, 1911.

N. natans (Bigelow, 1911).

N. spinosa Sears, 1952.

N. thetis Bigelow, 1911.

Familia Hippopodiidae: *Hippopodius hippopus* (Forskål, 1726).
Vogtia kuruae Alvariño, 1967.
V. pentacantha Kölliker, 1853.
V. serrata (Moser, 1913).
V. spinosa Keferstein & Ehlers, 1961.

Familia Diphyidae

Sub-familia Sulculeolariinae: *Sulculeolaria biloba* (Sars, 1846).
S. chuni (Lens & van Riemsdijk, 1908).
S. monoica (Chun, 1888).
S. quadrivalvis Blainville, 1834.

Sub-familia Diphyinae: *Chelophyes appendiculata* (Eschscholtz, 1829).
C. contorta (Lens & van Riemsdijk, 1908).
Dimophyes arctica (Chun, 1897).
Diphyes bojani (Eschsholtz, 1829).
D. dispar Chamisso & Eysenhardt, 1821).
Diphyopsis mitra (Huxley, 1859).
Eudoxoides spiralis (Bigelow, 1911).
Muggiaea atlantica Cunningham, 1892.
Lensia achilles Totton, 1941.
L. ajax Totton, 1941.
L. baryi Totton, 1965.
L. campanella (Moser, 1925).
L. challengeri Totton, 1954.
L. conoidea (Keferstein & Ehlers, 1860).
L. cossack Totton, 1941.
L. exeter Totton, 1941.
L. grimaldii Leloup, 1933.
L. havock Totton, 1941.

L. hostile Totton, 1941.

L. hotspur Totton, 1941.

L. lelouveteau Totton, 1941.

L. multicristata (Moser, 1925).

L. reticulata Totton, 1954.

L. subtilis (Chun, 1886).

Familia Clausophyidae: *Clausophyes ovata* (Keferstein & Ehlers, 1860).

Chuniphyes multidentata Lens & van Riemskijk, 1908.

Familia Sphaeronectidae: *Sphaeronectes gracilis* (Claus, 1873, 1874).

Familia Abylidae

Sub-familia Abylinae: *Abyla haeckeli* Lens & van Riemskijk, 1908.

A. bicarinata Moser, 1925.

A. brownia Sears, 1953.

Sub-familia Abylopsinae: *Abylopsis eschscholtzi* (Huxley, 1859).

A. tetragona (Otto, 1823).

Bassia bassensis (Quoy & Gaimard, 1834).

Enneagonum hyalinum (Quoy & Gaimard, 1827).

tribuidas en los siguientes sub-órdenes, Familias y Sub-familias.

De las sesenta y ocho especies determinadas y aquí mencionadas, tres especies (*Muggiaea atlantica, Chelophyes appendiculata, Eudoxoides spiralis*) han sido ya estudiadas en Alvariño (1980). También se han estudiado y publicado los resultados en Alvariño (1985), sobre las especies del género *Lensia* correspondientes a estas colecciones de 1969 (*L. achilles, L. ajax, L. baryi, L. campanella, L. challengeri, L. conoidea, L. cossack, L. exeter, L. grimaldii, L. havock, L. hostile, L. hotspur, L. lelouveteau, L. multicristata, L. reticulata, L. subtilis*).

Según se ha indicado, se han observado en otros trabajos en las zona de California y Baja California y zonas adyacentes (Alvariño 1967a, 1967b, 1971, 1972a, 1972b, 1974, 1980, 1983b; Bigelow y Leslie, 1930) un total de sesenta y dos especies. Las especies observadas previamente en estas regiones y que no han sido obtenidas durante los cruceros de 1969 son: *Dromalia alexandri* Bigelow, *Sulculeolaria turgida* (Gegenbaur) *Lensia subtiloides* (Lens & van Riemskijk), *L. meteori* (Leloup), *Eudoxia macra* Totton, *Chuniphyes moserae* Totton, *Clausophyes galeata* Lens & van Riemskijk, *Crystallophyes amygdalina* Moser, *Heteropyramis maculata* Moser, *Ceratocymba leuckarti* (Huxley), *C. dentata* (Bigelow).

Las especies determinadas en las colecciones de 1969 y que no se observaron en trabajos realizados previamente en las regiones de California y Baja California son: *Apolemia uvaria, Agalma elegans, Nanomia cara, Erenna richardi, Moseria convoluta, Athorybia rosacea, Forskalia edwardsi, Rosacea cymbiformis, Desmophyes annectens, Nectopyramis spinosa, Vogtia serrata, Sulculeolaria biloba, S. monoica, Lensia baryi, L. cossack, L. exeter, Sphaeronec-*

tes gracilis, Abyla brownia, Enneagonum hylinum.

Algunas especies presentan una distribución frecuente y abundante, pero la mayor parte de los sifonóforos debido a su comportamiento particular en desplazamiento y natación, se consideran raros, ya que se obtienen esparcidos en tiempo y espacio (Alvariño, 1983b; Alvariño *et al.*, 1990; Sears, 1953), y son hábiles para evadir las redes de plancton y no ser capturados.

Las especies más abundantes y frecuentes han sido, *Mugiaea atlantica, Chelophyes appendiculata* y *Eudoxoides spiralis*, a las cuales siguen en menor abundancia y frecuencia, *Agalma okeni, Stephanomia bijuga, Physophora hydrostaticas, Amphicaryon acaule, A. ernesti, Hippopodius hippopus, Vogtia kuruae, Sulculeolaria monoica, S. quadrivalvis, Diphyes bojani, D. dispar, Chuniphyes multidentata, Clausophyes ovata, Sphaeronectes gracilis*. Hay que tener en cuenta en estos estudios el comportamiento particular de los sifonóforos, ya que se ha observado (Alvariño, 1981, 1983b; Alvariño *et al.*, 1990; Biggs, 1977; Biggs *et al.*, 1981; Hamner *et al.*, 1975; Sears, 1953) que las características de natación y velocidad de desplazamiento de los sifonóforos permiten que estos organismos eviten ser capturados en los arrastres de las redes de plancton (Biggs, 1977) dando lugar a que los resultados obtenidos con el análisis de las muestras desplieguen una distribución irregular, en grupos y unidades dispersas por el ámbito oceánico.

La abundancia de las especies se analiza a continuación en relación con la distribución batimétrica diurna y nocturna en las cuatro estaciones del año 1969, considerando las fases poligástrica y eudoxia.

En la discusión detallada se sigue el orden sistemático y para las especies dentro de este orden se sigue en general el alfabético.

Las figuras 1 a, b, c y d presentan el plan general de estaciones y arrastres batimétricos para las cuatro estaciones del año, respectivamente, invierno (6902-03), primavera (6905-06), verano (6908-09) y otoño (6911-12).

Los datos numéricos detallados para las especies aquí discutidas, se presentan en la Tabla 1, ya que para las otras diez y nueve especies ya han sido publicadas en Alvariño 1980 y 1985.

Epibulia ritteriana se observó en invierno y verano. Esta especie descrita por Haeckel en 1888, la habían incluido Totton y Bargmann (1965) entre "species inquirenda". Alvariño (1974) describe un ejemplar capturado en un arrastre neuston en aguas de California, y también en el Atlántico sur se determinaron varios ejemplares (Alvariño, 1972a, 1981). Se trata de una especie epipelágica que habita los estratos más cercanos a la superficie oceánica. Todas las determinaciones de 1969 corresponden a estaciones en las enfilaciones 70 y 90. Así, en invierno se obtuvieron dos ejemplares de día en la estación 90.45 en un arrastre de 25-15 m de profundidad, y 2 ejemplares de noche en un arrastre de 15-0 m.

En el verano se determinó un total de 7 ejemplares, distribuidos en las estaciones 70.90, 90.45 y 90.60. En la estación 70.90 se obtuvo un ejemplar de noche. En la estación 90.45 se obtuvieron de día 3 ejemplares, uno en el arrastre de 25-0 m y 2 en el arrastre de 50-75 m, y uno de noche en los estratos de 25-0 m. En la estación 90.60 se obtuvo un ejemplar de día y otro de noche en los estratos entre 50-25 m de profundidad.

En invierno los ejemplares obtenidos de noche correspondían a estratos más profundos, pero en el verano no se ha establecido esa relación de profundidad con el período del día. La abundacia detallada de esta especie se presenta en la Tabla 1.

Apolemia uvaria se ha observado solamente en las colecciones de invierno, cuando se obtuvo un total de 20 ejemplares en la estación 90.60. Dos individuos se determinaron de día en las colecciones de 75-50 m y 22-11 m, y 18 ejemplares fueron capturados en un arrastre nocturno a 100-75 m de profundidad.

Agalma okeni se ha observado en las cuatro estaciones del año. Un total de 36 ejemplares y 163 larvas. Esta especie estaba distribuida por las estaciones en las tres enfilaciones, aunque en el invierno solamente se obtuvo en las enfilaciones 90 y 120. En la estación 90.45 se determinaron 9 larvas de noche en un arrastre de 25-15 m de profundidad. En la estación 90.60 se obtuvo un ejemplar en el estrato de 11-0 m; en la estación 120.55 se capturaron de noche 6 ejemplares distribuidos en arrastres a varios niveles de profundidad entre 100 y 0 m, en la estación 120.70 se observaron 4 ejemplares de noche en cuatro estratos entre 75 y 0 m, y en la estación 120.90 se obtuvieron 6 ejemplares y 4 larvas de noche en los varios estratos entre 75 y 0 m y de día se determinaron 2 ejemplares para cada uno de los estratos 100-75 y 300-250 m de profundidad.

En la primavera, 40 larvas se determinaron en un arrastre diurno en la estación 70.90 a 225-100 m de profundiad. En la estación 90.60 se determinaron 100 larvas de noche (50-25 m) y 5 larvas de día (50-25 m) y un ejemplar adulto de noche (50-25 m). En la estación 90.90 se obtuvieron 2 ejemplares de noche (25-0 y 75-50 m). En la estación 120.55 un ejemplar de noche (50-25 m) y en la estación 120.90, 3 ejemplares, uno de día (475-350 m) y 2 de noche en los arrastres entre 75 a 25 m de profundidad.

En el verano se obtuvieron adultos y larvas en la estación 70.60 de noche, en arrastres entre 475 y 350 m y 2 ejemplares de noche en la estación 120.70 en dos arrastres entre 75 y 25 m de profundidad.

En el otoño solamente se observó en la enfilación 120. Así, en la estación 120.70 se determinaron 2 ejemplares en dos arrastres de día entre 75 y 25 m de profundidad y un ejemplar en un arrastre nocturno entre 25-0 m de profundidad. En la estación 120.90 se capturaron 3 ejemplares de noche a 25-0 y 75-50 m.

Se ha observado que *A. okeni* es más frecuente en las estaciones de las enfilación 120. Además hay que indicar que *A. okeni* es una especie bastante frecuente en aguas de California y Baja Califoria, aunque no se observó en las colecciones obtenidas frente a San Diego (Alvariño, 1967b).

Stephanomia bijuga está representada en las cuatro estaciones del año, con ejemplares adultos y larvas. Esta especie se observó en las estaciones distribuidas en las tres enfilaciones, 70, 90 y 120.

En el invierno en la enfilación 70, se obtuvieron 7 larvas (estación 70-60) durante la noche a 50-25 m de profundidad y 2 adultos de día a 75-50 y 208-160 m de profundidad. En la estación 70-75 se capturaron de noche dos adultos a 15-0 y 25-15 m de profundidad. En la estación 90.60 se obtuvieron 50 larvas en un arrastre diurno a 50-34 m de profundidad y un adulto a 100-75 m. En la estación 120.90 se determinó de noche un adulto a 25-15 m de profundidad.

En la primavera el número de larvas capturadas ascendió a 85, y 16 adultos, distribuidos por las estaciones 70.60, 70.75 y 90.60. Las fases larvales se observaron a varias profundidades entre 100 y 0 m, presentándose más abundantes en las colecciones nocturnas que en las diurnas. Los adultos se observaron en varios estratos entre 475 y 25 m y también resultaban más abundantes en los arrastres nocturnos que en los diurnos (Tabla 1).

En el verano esta especie se determinó en las colecciones obtenidas a lo largo de las enfilaciones 70 y 90. Se capturó un total de 387 larvas y 10 adultos en esas estaciones. 250 larvas y 5 adultos distribuidos por las estaciones de la enfilación 70 y 137 larvas y 5 adultos en las estaciones de la enfilación 90, aún cuando la mayor parte de los ejemplares correspondían a las estaciones de la enfilación 70. En las estaciones de esta enfilación las larvas se obtuvieron durante el día en los estratos entre 350 y 100 m, y en las colecciones nocturnas entre 475 y 50 m. Los adultos se obtuvieron de día entre 350 y 25 m. En la enfilación 90, las larvas se extendían de día entre 475 y 350 m y de noche entre 475 y 75 m de profundidad. Se obtuvieron 5 adultos de día entre 475 y 50 m. En la estación 90.45 se determinaron 2 adultos, uno en cada uno de los arrastres entre 100 y 50 m. En la estación 90.60 se obtuvieron 3 en los estratos 475-350 m. La mayor parte de las larvas fueron capturadas de noche.

En el otoño disminuye la abundancia. Se obtuvo un total de 25 larvas y 10 adultos. En la estación 70.60 se observaron de noche las larvas distribuidas en los cuatro estratos entre 600 y 100 m de profundidad, siendo más abundantes en el estrato más profundo (600-475 m). Dos adultos se capturaron de día, uno a 475-350 m y otro a 50-25 m y 3 de noche, uno para cada estrato entre 75 y 0 m. En la estación 70.75 se observaron 3 ejemplares de día (2 a 225-100 m y 1 a 350-225 m de profundidad). En la estación 90.45 se obtuvo un ejemplar de noche a 225-100 m y en la estación 120.90 un ejemplar de noche a 225-100 m de profundidad.

Stephanomia bijuga era más abundante en el verano, disminuyendo en la primavera y con mínimos en el otoño e invierno. La reproducción parece ser continua en el año aunque con máximos en el verano y la primavera (Tabla 1).

Frente a San Diego, Cal., se observó (Alvariño 1967b) de día a 401-525 m, 110-0 m de profundidad y de noche a 410-460 y 235-300 m de profundidad. Otros datos sobre la distribución batimétrica de esta especie se puede obtener en Alvariño (1971).

Stephanomia rubra, Agalma elegans, Erenna richardi, Nanomia cara y *Moseria convoluta* están representadas por un solo ejemplar cada una, *S. rubra* y *M. convoluta* se observaron en el otoño, respectivamente en los arrastres diurnos en la estación 90.90 a 475-350 m de profundidad, y en la estación 90.60 a 350-225 m de profundidad.

A. elegans se observó en la primavera en un arrastre diurno a 100-75 m (estación 70.90). *Erenna richardi* y *Nanomia cara* se obtuvieron en las colecciones diurnas del verano, respectivamente en la estación 70.90 (arrastre a 75-50 m) y en la estación 90.90 (a 600-475 m de profundidad).

Stephanomia rubra se determinó frente a San Diego a 250-350 m de profundidad durante arrastres diurnos. (Alvariño, 1967b).

Bargmannia elongata se determinó solamente en primavera y verano. En la primavera se capturaron 15 ejemplares, 5 en la estación 70.60 (arrastre diurno a 475-350 m) y 10 en la estación 90.45, en un arrastre nocturno a 225-100 m de profundidad.

En el verano se observó un total de 194 ejemplares distribuidos por las tres enfilaciones de estaciones. En la estación 70.90 se obtuvieron 5 ejemplares de día a 350-225 m de profundidad, y 100 ejemplares de noche en la estación 70.75 en un arrastre entre 350-225 m de profundidad. En la estación 90.90 se determinaron 9 ejemplares de noche (600-475 m) y en la estación 120-70 también de noche se obtuvieron 70 ejemplares a 475-350 m de profundidad.

En general *B. elongata* se presenta en las colecciones de noche más abundante y en los estratos menos profundos durante este periodo.

Frente a San Diego, California, se obtuvo entre 250 m y 525 m durante el día y a varios niveles (235-300, 410-460, 860-1030, 1090-1242) de noche. También se ha observado en las islas de Cabo Verde a 370-0 m (Totton, 1954) y en el Mar de la China a 115 m de profundidad (Alvariño, 1971).

Physophora hydrostatica se observó distribuida en las colecciones de las cuatro estaciones del año. En el invierno y otoño se presentaba en las estaciones de las tres enfilaciones, pero en la primavera y verano solamente se capturó en estaciones de las enfilaciones 70 y 90. En el invierno se determinaron 21 ejemplares distribuidos en los estratos entre 130 y 0 m de profundidad, en la estación 70.75 (un ejemplar en las colecciones diurnas a 75-50 m de profundidad), en la estación 90.45 (3 ejemplares en las colecciones diurnas), distribuidos en los estratos entre 130 m y 0 m. En la estación 90.60 (4 ejemplares en las colecciones nocturnas, distribuidos en varios estratos entre 100 y 0 m), y 1 ejemplar se determinó de noche en la estación 120.70 a 50-25 m de profundidad.

En la primavera se observaron 2 ejemplares, uno en la estación 70.60 (arrastre nocturno a 100-75 m de profundidad), y otro en la estación 90.60 (arrastre diurno a 75-50 m).

En verano se obtuvieron 41 ejemplares distribuidos en 4 localidades. La mayor abundancia (36) se determinó en la estación 70.90 en un arrastre diurno a 100-75 m de profundidad. El resto de los ejemplares correspondían, a uno por arrastre (Tabla 1).

En el otoño se determinaron 16 ejemplares, 11 en la estación 70.60 distribuidos, 5 en un arrastre diurno (600-475 m de profundidad), 6 en arrastres nocturnos (5 a 600-475 m y 1 a 25-9 m). En la estación 90.45 se obtuvieron 3 ejemplares en arrastres nocturnos a 25-0 m y 75-50 m de profundidad. En la estación 120.90 se determinó de noche un ejemplar a 50.25 m de profundidad.

En la zona de San Diego se observó a 250-350 m de profundidad de día (Alvariño, 1967b).

Información adicional sobre la distribución batimétrica de esta especie se puede obtener en Alvariño (1971).

En general se observa, que la mayor abundancia de *Physophora hydrostatica* se ha obtenido en los arrastres nocturnos.

Athorybia rosacea y *Forskalia edwardsi* estaban representadas respectivamente por 7 y 2 ejemplares. Los 7 ejemplares de *A. rosacea* se observaron en el verano en un arrastre nocturno en la estación 90.60 a 50-25 m de profundidad, y *F. edwardsi* se determinó en la primavera en la estación 90.60 en arrastres diurnos, observándose un ejemplar en cada uno de los arrastres a 600-475 y 475-350 m de profundidad.

La sub-familia Amphicaryoninae estaba representada por *Amphicaryon acaule* y *A. ernesti*, que se encontraron únicamente en las colecciones de primavera, verano y otoño. *A. acaule* incluía 53 ejemplares en la primavera, 63 en el verano y 5 en el otoño y *A. ernesti* estaba representado por dos ejemplares en la primavera, 83 en el verano y 3 en el otoño. *A. acaule* se extendía en la primavera entre los 350 m y 25 m de profundidad, en el verano entre los 225 m y 25 m y en el otoño entre los 100 m y 25 m de profundidad. *A. ernesti* se observó en la primavera entre 75 m y 50 m, en el verano entre 475 m y 50 m, y en el otoño entre 100 m y 25 m de profundidad. Tabla 1.

A. acaule era más abundante que *A. ernesti* en la primavera y en el otoño, mientras que *A. ernesti* era más abundante en el verano. Sin embargo, *A. acaule* presentaba mayor frecuencia que *A. ernesti* en las tres estaciones del año 1969.

A. acaule se observó frente a San Diego de noche a 690-840 m y *A. ernesti* a 20-100 m también de noche. Otros datos sobre la distribución batimétrica de estas especies se incluyen en Alvariño (1971).

Rosacea plicata se observó en las colecciones de primavera y verano y *R. cymbiformis* en las de primavera, verano y otoño. *Rosacea plicata* estaba representada por un ejemplar en cada una de las localidades 70.60, 70.75, 90.60 y 90.90 durante la primavera en los estratos respectivamente de 350-225, 475-350 (arrastres nocturnos), y a 50-25 m (arrastres diurnos) y a 25-0 m en un arrastre nocturno.

En el verano se observaron 5 larvas de *R. plicata* en cada una de las localidades 90.60 y 120.55 (475-350 m de profundidad) en arrastres diurnos. En esta estación se obtuvieron 46 ejemplares distribuidos en las estaciones 70.90, 70.110, 90.60, 120.55, 120.90. Lo ejemplares se determinaron principalmente en los estratos 350-225 m y 475-350 m en arrastres diurnos y nocturnos, excepto en la estación 70.90 donde se obtuvo un ejemplar a 75-50 m de profundidad en una arrastre diurno. La hora del arrastre no marcó variación en la abundancia ni en la profundidad (Tabla 1).

Sin embargo, *R. plicata* fue observada frente a San Diego de día a 2210-2630 m de profundidad, mientras que de noche se capturó en estratos menos profundos, 235-300 y 410-460 m (Alvariño, 1967b). Más información sobre la distribución batimétrica se puede encontrar en Alvariño (1971).

Rosacea cymbiformis estaba representada en la primavera por un ejemplar en la estación 70.60, en un arrastre diurno a 25-0 m. En el verano se obtuvieron 10 ejemplares de la fase poligástrica y 5 eudoxias en la estación 120.70 en un arrastre diurno a 475-350 m de profundidad, y en el otoño en la misma localidad y profundidad y período del día se obtuvo un ejemplar. Tabla 1.

En todos los casos, salvo la excepción indicada, tanto para *R. plicata* como *R. cymbiformis*, los ejemplares correspondían a la fase poligástrica.

Nectodroma dubia se observó en la primavera, verano y otoño, representada por un ejemplar en cada una de las muestras. En la primavera se observó en la estación 70.75 de día a 100-75 m y de noche a 50-25 m de profundidad. En el verano se obtuvo en la estación 70.110 a 25.0 m de noche y en la estación 120.55 a 350.225 m de día. En el otoño se observó en la estación 225-100 m de profundidad de noche.

Según estos datos, *N. dubia* se extiende por amplios estratos batimétricos y se ha obtenido de noche a menor profundidad que durante el día. Tabla 1.

En la zona de San Diego se extendía entre 460-0 m de profundidad durante el día (Alvariño, 1967b). Información sobre la distribución batimétrica de esta especie se presenta en Alvariño (1971).

Nectodroma reticulata se obtuvo en las colectas de invierno, verano y otoño. En el invierno se determinó en la estación 70.75 un ejemplar en cada uno de los arrastres diurnos a 350-225 m y 75-50 m de profundidad y en la estación 90.45 a 60-50 m se obtuvo un ejemplar en un arrastre diurno. En el verano se observó en la estación 70.90 un ejemplar en un arrastre nocturno a 50-25 m de profundidad, en la estación 90.60 dos ejemplares en un arrastre diurno a 475-350 m y en la estación 120.45 un ejemplar en un arrastre nocturno a 225-100 m de profundidad. En el otoño solamente se obtuvieron 2 ejemplares en la estación 120.70 en un arrastre nocturno a 350-225 m de profundidad. Tabla 1.

En San Diego se observó de día a 350-250 m y 1720-1340 m de profundidad y de noche a 100-20 m de profundidad (Alvariño, 1967b). En estas colecciones la especie habitaba estratos notablemente menos profundos de noche que durante el día.

Desmophyes annectens se observó en el invierno en la estación 90.55 (arrastre nocturno a 168-130 m de profundidad), y en la primavera en la estación 70-75 (arrastre diurno a 600-475 m de profundidad). Tabla 1.

Nectocarmen antonioi estuvo representado por un ejemplar en la primavera, en la estación 90.60 en un arrastre diurno a 75-50 m de profundidad. Tabla 1.

La sub-familia Nectopyramidinae estaba representada por las cuatro especies que la integran. La especie más frecuente y abundante ha sido *Nectopyramis diomedeae*, con 9 ejemplares obtenidos en las colecciones de primavera, verano y otoño. Esta especie se presentó en los estratos entre 600 y 350 m de profundidad (Tabla 1), y no se observaron variaciones en la profundidad en relación con la hora del arrastre.

Alvariño (1967b) ha observado *N. diomedeae* frente a San Diego, a 410-460 y 685-775 m en arrastres nocturnos.

Nectopyramis natans, N. spinosa y *N. thetis* se obtuvieron respectivamente en la primavera y verano, y las dos últimas en la primavera. Cinco ejemplares de *N. natans* se observaron en la estación 120.90 a 475-350 m de profundidad en un arrastre diurno, y las otras dos especies estuvieron representadas por un ejemplar solamente. Tabla 1.

Frente a San Diego solamente se obtuvo de este trio de especies *N. thetis* en un arrastre nocturno a 860-1030 m de profundidad (Alvariño, 1967b). Datos sobre la distribución batimétrica de las cuatro especies de Nectopyramidinae se detallan en Alvariño (1971).

La Familia Hippopodiinae estaba representada por cinco especies, ya que *Vogtia glabra* no se ha observado en estas colecciones. Las especies más abundantes y frecuentes han sido en orden decreciente, *Vogtia kuruae* e *Hippopodius hippopus*, seguidas por las otras tres especies.

Hippopodius hippopus se observó en las cuatro estaciones del año. En el invierno se presentaba en las estaciones 90.45 y 90.60 en arrastres respectivamente nocturnos y diurnos a 130-95 y 100-75 m de profundidad. En la primavera en las estaciones 90.60 y 90.90 en varios arrastres entre 100 m y 25 m de profundidad. En el verano en tres localidades (70.110, 90.90 y 120.70) y en el otoño también en tres localidades (90.45, 90.60, 90.90) en varios estratos entre 75 y 0 m. Tabla 1.

H. hippopus en general se observó a menor profundidad en las colecciones nocturnas que en las diurnas.

Vogtia kuruae se obtuvo en primavera, verano y otoño. En estas colecciones se capturó un total de 60 ejemplares. En la primavera se determinaron 26 ejemplares en tres localidades en los estratos entre 600 y 475 m de profundidad. En el verano se obtuvieron 24 ejemplares distribuidos en 6 estaciones en colecciones obtenidas en los estratos entre

475-350 m de profundidad, y en el otoño se obtuvieron 24 ejemplares distribuidos en seis estaciones en colecciones obtenidas en los estratos entre 475-350 m de profundidad, y en el otoño se observaron 10 ejemplares en 4 estaciones de arrastres entre 475 m y 350 m de profundidad, con una observación en la estación 120.55 a 25.0 m en un arrastre nocturno. Tabla 1.

Según estos datos, *V. kuruae* se presentaba a mayor profundidad en la primavera que el resto de las estaciones, y no se observaron variaciones en abundancia en relación con la hora del arrastre. Tabla 1.

En la zona de San Diego se observó a 525-401 y 1720-1340 m de profundidad de día y a varios niveles entre 1030 m y 420 m de noche (Alvariño, 1967b).

Vogtia pentacantha se observó en el invierno, verano y otoño, con un total de 8 ejemplares obtenidos en los estratos entre 600 y 225 m de profundidad. Tabla 1.

Vogtia serrata se determinó en las colecciones de primavera, verano y otoño, con 12 ejemplares obtenidos a 600-475 m de profundidad. Tabla 1.

Vogtia spinosa estuvo representada por 10 ejemplares distribuidos en el invierno en estratos 350-225 m en la primavera a 475-350 m, y en el verano entre 225-100 m de profundidad (Tabla 1). Datos adicionales sobre la distribución batimétrica de las especies de la Familia Hippopodiidae están recopilados en Alvariño (1971).

La sub-familida Sulculeolariinae incluye un total de ocho especies (Alvariño, 1968), pero en las colecciones de 1969 estuvo representada por cuatro especies en sus respectivas fases poligástricas. *Sulculeolaria quadrivalvis* ha sido la especie más abundante y frecuente en estas colecciones, seguida por *S. monoica*, mientras que *S. biloba* y *S. chuni* estaban representadas por un solo ejemplar cada una, en las colecciones de verano (Tabla 1).

Suculeolaria monoica se obtuvo en las las cuatro estaciones del año. En general, esta especie ha sido observada en los estratos entre 100 m y 0 m excepto en el invierno cuando un solo ejemplar se obtuvo en la estación 120.90 en un arrastre diurno a 225-200 m de profundiad. En la primavera se observó solamente en las estaciones 90.60, 90.90. En el verano se obtuvo en las localidades más océanicas de las tres enfilaciones (70.110, 90.90, 120.70), y en el otoño se determinó en las enfilaciones más meridionales (90.60, 90.90, 120.90).

Esta especie ha sido más abundante en el verano, seguido por el otoño, con mínimos en el invierno y primavera (Tabla 1).

Sulculeolaria quadrivalvis estaba representada por 22 ejemplares en el invierno, distribuidos por las estaciones 70.60, 90.60, 120.70, 120.90, en arrastres entre 120 y 0 m. Esta especie se presentaba abundante en las estaciones más meridionales. En la primavera se obtuvieron 29 ejemplares distribuidos por las estaciones 70.60, 70.75, 70.90, 90.60, 90.90, 120.45, en varios estratos entre 100 m y 0 m. En el verano se obtuvieron 33 ejemplares en las localidades más océanicas de la enfilación 70, en estratos entre 350 m y 25 m de profundidad. En el otoño se determinaron 81 ejemplares distribuidos por las estaciones 90.60, 90.90 y 120.90 en arrastres entre 475 m y 0 m. Esta especie ocupaba estratos menos profundos en la primavera, habitando en general las localidades más oceánicas de la zona explorada. Tabla 1.

Información detallada sobre la distribución batimétrica de estas especies del género Sulculeolaria puede obtenerse en Alvariño (1971).

La sub-familia Diphyinae estaba representada por las siguientes especies: *Chelophyes appendiculata, C. contorta, Dimophyes arctica, Diphyes bojani, D. dispar, Diphyopsis mitra, Eudoxoides spiralis, Muggiaea atlantica.*

Las especies más abundantes y frecuentes en este grupo que se obtuvieron en las colecciones de 1969, *Chelophyes appendiculata, Eudoxoides spiralis, Muggiaea atlantica* ya han sido estudiadas y discutida su distribución batimétrica y las épocas de reproducción en Alvariño (1980).

Chelophyes contorta es una especie pareja de *C. appendiculata*. Aquella es una especie restringida a las aguas tropicales, mientras que la última es abundante en las zonas templadas oceánicas. (Alvariño 1971, 1974). Ejemplares de la fase poligástrica de *C. contorta* se obtuvieron en el invierno en la estación 120.70 a profundidades entre 75 m y 0 m en colecciones diurnas y entre 50 m y 0 m de noche. La población obtenida en los arrastres nocturnos era más abundante que la de los diurnos y ocupaba asimismo estratos menos profundos en este período del día.

La presencia de *C. contorta* en esta época del año (invierno) y localidad (120.70) oceánica, está favorecida por el flujo hacia el norte de las aguas cálidas en esta época del año. (Alvariño 1983a). En las colecciones de 1969 se ha observado que la especie era más abundante en las muestras obtenidas durante la noche. Tabla 1.

Dimophyes arctica se observó en el invierno en la estación 90.60, tres ejemplares en un arrastre diurno entre 176-100 m de profundidad y 10 ejemplares en el verano en la estación 70.110 en un arrastre diurno a 475-350 m de profundidad. Esta especie ocupa los estratos epipelágicos en las altas latitudes y desciende a los estratos profundos oceánicos en las latitudes medias y bajas. Tabla 1.

Frente a San Diego se observó de día a 2630-2210 m de profundidad y de noche a 420-410m de profundidad (Alvariño, 1967b).

Se han obtenido ejemplares de *Diphyes bojani* en la fase poligástrica durante las cuatro estaciones del año y de la fase eudoxia solamente en la primavera, verano y otoño. En el invierno se observaron ejemplares de la fase poligástrica en las estaciones 70.75 y 120.90 a profundidades entre 50 m y 25 m. En la primavera se obtuvieron 169 ejemplares de la fase poligástrica y 441 de la fase eudoxia. La fase poligástrica se obtuvo en las estaciones 70.90 y 90.90 y la de eudoxia en las estaciones 70.110, 90.90. La fase poligástrica habitaba los estratos entre 50 m y 0 m, y la fase eudoxia entre 100 m y 0 m. Durante esta estación se observaron más eudoxias en las colecciones diurnas, mientras que la fase poligástrica era más abundante en las colecciones nocturnas. En general, en esta estación las fases de eudoxia se extendian hacia estratos más profundos, probablemente debido al menor potencial natatorio y que las gónadas incrementan la densidad de los ejemplares, disminuyendo su flotabilidad.

En el verano se obtuvieron 13 ejemplares de la fase poligástrica y 77 de la fase eudoxia, distribuidos por las estaciones 70.110, 90.60, 90.90. La fase poligástrica habitaba estratos entre 50 m y 0 m y la fase eudoxia entre 75 m y 25 m de profundidad. También en el verano la fase eudoxia ocupaba estratos más profundos que la fase poligástrica.

En el otoño se determinaron 1160 ejemplares de la fase poligástrica y 593 de la fase eudoxia, distribuidos por las estaciones 90.90 y 120.90. Ejemplares correspodientes a la fase poligástrica y eudoxia ocuparon los estratos entre 225 m y 0 m.

D. bojani era más abundante en el otoño tanto en la fase eudoxia como en la fase poligástrica, decreciendo en la primavera, con mínimos en el verano, mientras que en el invierno la fase eudoxia estaba ausente. En el otoño se observó una reproducción más intensa, seguida por la primavera, disminuyendo en el verano y en el invierno no se observó evidencias de reproducción (Tabla 1). Información adicional sobre la distribución batimétrica de *D. bojani* se incluye en Alvariño (1971).

Diphyes dispar es la especie más abundante y frecuente en las colecciones después de las tres especies (*Chelophyes appendiculata, Eudoxoides spiralis, Muggiaea atlantica*) que ya han sido estudiadas (Alvariño, 1980).

Diphyes dispar estaba representada por ejemplares de las fases poligástricas y de eudoxia, en las cuatro estaciones del año.

En el invierno se obtuvieron 130 ejemplares poligástricas en las estaciones 70.60, 70.75, 120.45, 120.90 y 213 eudoxias en la estación 120.90. La fase poligástrica se extendía por los estratos entre 100 m y 0 m y las eudoxias entre los 100 m y 75 m de profundidad.

En la primavera se determinaron ejemplares de la fase poligástrica en las estaciones 90.90 y 120.45 y 403 eudoxias en la estación 90.90. La fase poligástrica habitaba los estratos entre 75 m y 0 m y las eudoxias entre 75 m y 50 m de profundidad.

En el verano se obtuvieron 210 ejemplares de la fase poligástrica en las estaciones 90.60, 90.90, 120.55, 120.70, 120.90 y 33 eudoxias distribuidas por las estaciones 90.60, 90.90, 120.55, 120.70. La fase poligástrica ocupaba los estratos entre 350 m y 0 m y las eudoxias se capturaron en los estratos entre 50 m y 0 m de profundidad. En esta estación se observa que la fase de eudoxia habitaba estratos menos profundos que los ejemplares de la fase poligástrica, a diferencia del invierno y primavera cuando en general las eudoxias habitaban estratos más profundos que la fase poligástrica.

En el otoño se determinaron 287 ejemplares de la fase poligástrica y 1917 eudoxias distribuidas por las estaciones 70.60, 90.45, 90.60, 90.90, 120.55, 120.70, 120.90. Las fases poligástricas y de eudoxia habitaban los estratos entre 225 m y 0 m. Tabla 1.

La reproducción de *D. dispar* se presentaba más intensa en el otoño. En la primavera e invierno la población reproductora de eudoxias, era mayor que la población poligástrica, mientras que en el verano la población poligástrica era mayor que la de eudoxias, que alcanzó el mínimo del año en esta estación. Por lo tanto, según los datos, el auge de la reproducción se produjo en el otoño, seguido por la primavera e invierno, mientras que en el verano se observó el mínimo en este proceso del ciclo vital. Información sobre la distribución batimétrica de *D. dispar* está recopilada en Alvariño (1971).

Diphyopsis mitra estaba representada por poblaciones de las fases poligástrica y eudoxia en el invierno, primavera y verano. Esta especie no se observó en las colecciones del otoño.

En el invierno se obtuvieron 137 ejemplares de la fase poligástrica y 158 eudoxias, distribuidos por las estaciones 90.60, 120.70, 120.90. La fase poligástrica habitaba los estratos entre 50 m y 15 m de profundidad y las eudoxias se capturaron en los estratos entre 120 m y 15 m de profundidad. En esta estación las eudoxias habitaban estratos más profundos que la fase poligástrica, siguiendo así el patrón observado también para otras especies estudiadas más arriba.

En la primavera se observaron 68 ejemplares de la fase poligástrica en la estación 70.110 a 100-75 m de profundidad y 75 eudoxias que se extendían por los estratos entre 100 y 25 m de profundidad.

En el verano no se observaron ejemplares de la fase poligástrica y solamente se capturaron 133 eudoxias en la estación 70.110, 5 ejemplares se obtuvieron de día a 350-225 m de profundidad y 128 de noche en el mismo estrato.

Como en los casos anteriores, en general las eudoxias habitaban estratos más profundos que la fase poligástrica. Tabla 1.

En Alvariño (1971) se incluye información sobre la distribución batimétrica de *D. mitra* en los océanos Atlántico, Pacífico e Índico.

La reproducción de *D. mitra* se presentaba más activa en el invierno, cuando se observaron poblaciones abundantes de las fases poligástrica y de eudoxia. En el verano también existía una reproducción activa, habiendo desaparecido la población de la fase poligástrica, y en la primavera las poblaciones de ambas fases eran escasas. En el otoño la especie estaba ausente de la región.

Esta especie es de régimen epipelágico y en general se presentaba más abundante en las localidades más alejadas de la costa. *D. mitra* es una especie abundante en las zonas templadas y cálidas oceánicas y su mayor abundancia en California en el invierno se debe a la influencia de la corriente cálida que avanza por esta región, así las poblaciones encontradas en verano en la zona mesopelágica son probablemente el resultado de la sumersión de las aguas que habitan. No obstante la reproducción es al parecer continua en la región, con máximos en el invierno, cuando existen poblaciones de ambas formas del desarrollo, y mínima en el verano, mientras que en el otoño no se capturaron en las colecciones representantes de esta especie.

Chuniphyes multidentata se ha presentado bastante abundante y frecuente en las regiones de California y Baja California durante 1969, principalmente en la primavera, verano y otoño, ya que en el invierno solamente se observaron 10 ejemplares de la fase poligástrica en la estación 90.45 en un arrastre nocturno a 168-130 m de profundidad.

En la primavera se determinó un total de 1244 ejemplares de la fase poligástrica en los arrastres nocturnos en las estaciones 70.60, 70.75, 70.90 y 70.110 y 700 en los arrastres diurnos en las estaciones mencionadas de la enfilación 70. Esta especie habitaba los estratos entre 600 y 100 m de profundidad. Se observaron 20 eudoxias en la estación 70.75 en un arrastre diurno entre 600-475 m de profundidad. En la enfilación 90 se capturaron 575 ejemplares de la fase poligástrica en los arrastres nocturnos y 85 en los arrastres diurnos, a profundidad entre 600 y 225 m y 75 eudoxias se obtuvieron en la estación 90.45 en un arrastre nocturno a 475-350 m de profundidad. En las estaciones de la enfilación 120 se obtuvieron 30 ejemplares de la fase poligástrica en arrastres nocturnos y 130 de día, a profundidades entre 600 y 225 m y 5 eudoxias se determinaron de noche en la estación 120.45 a 475-350 m de profundidad y 20 en un arrastre diurno a 600-475 m de profundidad. En la primavera tanto la fase poligástrica como de eudoxia se observaron a mayor profundidad en los arrastres diurnos que en los nocturnos.

En el verano se determinó un total de 305 ejemplares de la fase poligástrica en las estaciones de la enfilación 70, distribuidos 215 de noche y 90 de día. Estas poblaciones habitaban día y noche estratos entre 600 y 100 m de profundidad. Se obtuvo un total de 40 eudoxias en la enfilación 70, 20 en arrastres diurnos y 20 en arrastres nocturnos a profundiades entre 475 m y 350 m en ambos períodos. En la enfilación 90 se capturó un total de 245 ejemplares de la fase poligástrica, distribuidos 215 de día y 30 de noche, a profundidades entre 600 m y 350 m y 20 eudoxias se obtuvieron de noche a 600-475 m de profundidad en la estación 90.45. En la enfilación 120 se obtuvo un total de 115 ejemplares de la fase poligástrica distribuidos 40 para las colecciones nocturnas y 75 las diurnas. Estas poblaciones habitaban en los dos períodos del día los estratos entre 600 m y 225 m de profundiad. Se obtuvieron 25 eudoxias en la enfilación 120, 15 en arrastres diurnos y 10 en arrastres nocturnos, a profundidades entre 600 m y 350 m.

En el otoño se observó en las estaciones de la enfilación 70, una población representada por 600 ejemplares de la fase poligástrica, distribuidos 460 en las colecciones diurnas y 140 en las nocturnas. Estas poblaciones habitaban los estratos entre 600 m y 350 m de profundidad y 25 eudoxias se capturaron en la estación 70.75 en un arrastre diurno a 600 m y 475 m de profundidad. En la enfilación 90 se obtuvieron 290 ejemplares de la fase poligástrica y 5 eudoxias. Los ejemplares de la fase poligástrica se distribuían, 150 en los arrastres nocturnos y 140 en los diurnos, a profundidades entre 600 m y 225 m, y las eudoxias se obtuvieron en la estación 90.60 a 350-225 m en un arrastre diurno. En la enfilación 120 se determinaron 55 ejemplares de la fase poligástrica, distribuidos 40 de noche y 15 de día, a profundidades de 600-350 m. Tabla 1.

Chuniphyes multidentata presentaba mayor abundancia en la primavera y verano, y su reproducción también se mostraba con mayor actividad en estas estaciones. La falta de determinaciones en el invierno se debe a la característica de los arrastres en esta estación, cuando no abarcaron los niveles batimétricos que habita la especie.

C. multidentata es de régimen mesopelágico, y en general se aprecia que los ejemplares de la fase eudoxia habitaban particularmente estratos siempre más profundos, debido probablemente a la mayor densidad de los ejemplares a causa del peso de las gónadas y a una menor facultad natatoria.

En la zona de San Diego *C. multidentata* habitaba de día los estratos entre 525-401, 2300-1880 y 3040-2620 m de profundidad, mientras que de noche habitaba en general los estratos muestreados entre 420 m y 2460 m de profundidad (Alvariño, 1967b). Información adicional sobre la distribución batimétrica de esta especie está recopilada en Alvariño (1971).

Clausophyes ovata se observó en la primavera, verano y otoño, habitando en general los estratos entre 600 m y 350 m de profundidad. En el invierno no se capturó, ya que en esta estación no se exploraron los niveles batimétricos que habita la especie.

En la primavera se obtuvo un total de 280 ejemplares de la fase poligástrica distribuidos por las estaciones de las enfilaciones 70, 90 y 120, a profundidades entre 600 m y 350 m. En los arrastres diurnos se obtuvieron 175 ejemplares y 105 de noche. No se observaron eudoxias, y la mayor abundancia se obtuvo en las localidades a lo largo de las enfilaciones 70 y 90.

En el verano se capturaron 300 ejemplares de la fase poligástrica, distribuidos día y noche en los estratos entre 600 y 225 m de profundidad. En las colecciones diurnas se obtuvieron 130 y 170 en las nocturnas. En la estación 90.60 se observaron 15 eudoxias, 5 de ellas a 350-225 m y 10 a 475-350 m de profundidad en arrastres nocturnos y otras 5 eudoxias en la estación 120.45 en un arrastre de noche a 475-350 m de profundidad.

En el otoño se obtuvieron 225 ejemplares de la fase poligástrica a profundiades entre 600 m y 350 m. Durante el día se obtuvieron 85 y 140 de noche. No se determinaron eudoxias en esta estación. Tabla 1.

La mayor abundancia de *C. ovata* se determinó en el verano, estación en que se presenta la reproducción de la especie en las regiones exploradas. Según los datos obtenidos, la fase poligástrica en este caso habitaba en general estratos algo más profundos que las poblaciones de la fase eudoxia.

En la zona de San Diego *Clausophyes ovata* se observó en las colecciones diurnas en los estratos entre 1340 y 2630 m de profundidad y no se obtuvieron ejemplares en las colecciones nocturnas (Alvariño, 1967b).

Clausophyes ovata es una especie abundante en la región Subantártica y zonas adyacentes (Alvariño *et al.*, 1990). Información extensiva sobre la distribución batimétrica de *C. ovata* aparece recopilada en Alvariño (1971).

Sphaeronectes gracilis se capturó en invierno y primavera. En estas estaciones la especie estaba ausente de las localidades de la enfilación 70. En el invierno se determinó un total de 4971 ejemplares, 4919 de día a profundidades entre 100 m y 15 m, y 52 de noche a profundidades entre 40 m y 0 m. La especie ocupaba estratos más profundos de día que de noche.

En la primavera se obtuvo un total de 870 ejemplares en las estaciones 90.55 y 120.70 en colecciones nocturnas, habitando los estratos entre 100 m y 0 m de profunidad. Tabla 1.

La sub-familia Abylinae estaba representada por las siguientes especies: *Abyla bicarinata, A. brownia, A. haeckeli.*

Abyla bicarinata se observó esparcida en las colecciones de primavera, verano y otoño y siempre se obtuvo en arrastres nocturnos. En la primavera se determinó en la estación 90.60 un ejemplar de la fase poligástrica en el estrato de 50-25 m de profundidad. En el verano se observaron 3 ejemplares en la estación 90.90 a la misma profundidad que en la primavera y en el otoño se capturó un ejemplar en la estación 90.45 a 25-0 m de profundidad. Tabla 1.

Información adicional sobre la distribución batimétrica de *A. bicarinata* se incluye en Alvariño (1971).

Abyla brownia solamente se observó en el invierno, presentándose en la estación 90.60, en un arrastre diurno a 50-34 m de profunidad. Tabla 1.

Abyla haeckeli estaba representado solamente por ejemplares de la fase eudoxia, distribuidos en las colecciones de invierno, primavera, verano y otoño. En todos los casos se determinaron en las estaciones de la enfilación 90, excepto en el otoño cuando también se obtuvieron en la estación 120.90.

En el invierno, *A. haeckeli* ocupaba los estratos entre 75 m y 0 m de profundidad durante el día. En la primavera los estratos entre 75-50 m de noche y 50-25 m de día. En el verano ocupaba los estratos entre 50-0 m de noche y 75-0 m de día. En el otoño, tanto de día como de noche habitaba los estratos entre 50-0 m de profundidad. Tabla 1.

Las eudoxias eran más abundantes en el otoño y más escasas en la primavera, pero la mayor frecuencia correspondía al verano. Es notable la falta de ejemplares de la fase poligástrica de esta especie en todas las colecciones de 1969. Datos sobre la distribución batimétrica de *A. haeckeli* están recopilados en Alvariño (1971).

La sub-familia Abylopsinae estaba representada por cuatro de las cinco especies que integran este grupo, ya que *Enneagonum searsae* no se observó en las colecciones de 1969. Las especies determinadas en estas colecciones han sido: *Abylopsis eschscholtzi, A. tetragona, Bassia bassensis* y *Enneagonum hyalinum*. Estas especies son de régimen tropical, de modo que su presencia en aguas de California es esporádica.

En la pareja de especies del género *Abylopsis, A. eschscholtzi* esta más restringida a las aguas tropicales, mientras que *A. tetragona* también habita esta zona pero extiende su distribución hacia las aguas templadas adyacentes.

Abylopsis eschscholtzi se observó solamente en el verano y en la estación 90.90, donde se determinó un ejemplar en un arrastre diurno a 50-25 m de profundidad y 15 en un arrastre nocturno a 75-50 m de profundidad. Tabla 1.

Abylopsis tetragona se determinó en las colecciones de invierno, primavera, verano y otoño. En el invierno se obtuvieron 44 ejemplares de la fase poligástrica en la estación 120-90 (la más meridional y oceánica de la región explotada) , uno de noche a 15-0 m, otro de día a 50-25 m y 42 de día a 150-100 m de profundidad.

En la primavera, en la estación 90.90 se observaron 8 ejemplares de la fase poligástrica y 50 eudoxias, en un arrastre nocturno a 25-0 m de profundidad.

En el verano, en la misma estación 90.90, se obtuvieron 2 eudoxias en dos arrastres nocturnos, a 50-25 y 25-0 m de profundiad.

En el otoño también en la estación 90.90 se observaron en arrastres diurnos 114 ejemplares de la fase poligástrica y 361 eudoxias, de modo que 109 ejemplares de la fase poligástrica y las 361 eudoxias se distribuían por los estratos 100-75, 50-25 y 25-0 m de profundidad, y los otros ejemplares de la fase poligástrica habitaban los estratos entre 475-350 m de profundidad. Tabla 1.

Bassia bassensis se presentaba en la primavera, verano y otoño. Solamente se observaron ejemplares de la fase poligástrica. En la primavera se determinaron 8 en la estación 90.90, en un arrastre nocturno a 25-0 m de profundidad. En el verano se obtuvieron 17 ejemplares, uno en la estación 70.110 (25-0 m), otro en la estación 90.90 (50-25 m) y 15 en la estación 120.70 a 75.50 m de profundidad. En el otoño se capturó sólo un ejemplar en la estación 90.90 a 50-25 m de profundidad. Esta especie ocupaba estratos más profundos de día que de noche. Tabla 1.

Enneagonum hyalinum se determinó en la estación 120.90 (la más meridional y oceánica de la zona explorada) durante la primavera y el verano, en arrastres diurnos a 25-0 m de profunidad. Tabla 1.

Las especies de la sub-familia Abylopsinae son de régimen batimétrico epipelágico, habitando los estratos más profundos de esta región, y debido a su característica tropical su presencia en aguas de California y Baja California no incluye poblaciones abundantes. Información adicional sobre la distribución batimétrica de las especies de la sub-familia Abylopsinae se recopila en Alvariño (1971).

El género *Lensia* incluye un total de 27 especies, de las cuales 16 han sido en estas colecciones de 1969 y se discute su distribución estacional y batimétrica, así como su abundancia en Alvariño (1985).

Se observa en general que con alguna frecuencia las especies se presentan a niveles menos profundos de noche que de día. También se ha observado que en la mayor parte de las especies, los ejemplares de la fase eudoxia habitaban estratos más profundos que las poblaciones de la fase poligástrica.

Epibulia ritteriana, Apolemia uvaria, Agalma okeni, Physophora hydrostatica, Athorybia rosacea, Amphicaryon acaule, Nectocarmen antonioi, Hippopodius hippopus, Sulculeolaria biloba, S. monoica, S. quadrivalvis, Chelophyes contorta, Diphyes bojani, D. dispar, Diphoyopsis mitra, Sphaeronectes gracilis, Abyla bicarinata, A. brownia, A. haeckeli, Abylopsis eschscholtzi, A. tetragona, Bassia bassensis, Enneagonum hyalinum, pueden considerarse de régimen epipelágico en las regiones de California y Baja California. Hay además que incluir en la categoría de especies epipelágicas las estudiadas previamente en Alvariño (1980) (*Muggiaea atlantica, Chelophyes appendiculata, Eudoxoides spiralis*) y asimismo, *Lensia challengeri, L. cossack, L. hotspur, L. campanella, L. exeter, L. subtilis* (Alvariño, 1985).

Muchas de estas especies habitan los estratos menos profundos de la región epipelágica, mientras que otras (Agalmidae, Pyrostephidae) probablemente recorren en sus desplazamientos estratos amplios de las zonas epi-, meso- y batipelágicas.

En la categoría mesopelágica podían también incluirse las siguientes especies del género *Lensia* (Alvariño, 1985), *L. conoidea, L. multicristata, L. grimaldii, L. achilles, L. ajax, L. havock, L. hostile, L. lelouveteau, L. retriculata, L. baryi* que ya han sido estudiadas como se indica.

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REFERENCIAS

ALVARIÑO, A., 1967a. A new Siphonophore, *Vogtia kuruae* n. sp. *Pacific Science* 21(2):236-240 & *Contributions Scripps Institution of Oceanography* 37(2109):186-190.

---------- 1967b. Bathymetric distribution of Chaetognatha, Siphonophora, Medusae and Ctenophora off San Diego. *Pacific Science*, 21(4):474-485 & *Contributions of Scripps Institution of Oceanography* 37 (2171):902-913.

---------- 1968. Two new Siphonophora, Calycophorae. *Pacific Science*, 22(3):340-346 & *Contributions Scripps Institution of Oceanography* 38(2316):242-248.

---------- 1969. Zoogeografía del Mar de Cortés: Quetognatos, Sifonóforos y Medusas. *Anales de Instituto de Biología*. Universidad Nacional Autónoma de México, Serie Ciencia, Mar y Limnología (11):11-54.

----------1971. Siphonophores of the Pacific; with a revision of the World distribution. *Bulletin Scripps Institution of Oceanography*, University of California San Diego, La Jolla, California, 16:1-432. University of California Press.

---------- 1972a. A second record of the Siphonophore *Epibulia ritteriana* Haeckel 1888. *U.S. Fishery Bulletin*, 70(2):507-509.

---------- 1972b. Zooplancton del Caribe, Golfo de México y regiones adyacentes del Pacífico. Memorias IV Congreso Nacional de Oceanografía, México:223-247.

---------- 1974. Distribution of Siphonophores in the regions adjacent to the Suez and Panama Canals. U.S. *Fishery Bulletin*, 72(2):527-546.

---------- 1980. Reproduction seasons and day/night distribution of three species of Diphynae (Siphonophora) off California and Baja California. In: Tarden, P. & R. Tarden (Eds.), Proceedings 4th International Coelenterates Conference, September 1979, Interlaken, Switzerland . Developmental and Celular Biology of Coelenterates:33-38.

---------- 1981. Siphonophora. Atlas del Zooplancton del Atlántico Sudoccidental. Publicación del Instituto Nacional de Investigaciones y Pesca. Departamento de Comercio, Argentina:383-441.

---------- 1983a. The depth distribution, relative abundance and structure of the population of the chaetognatha *Sagitta scrippsae* Alvariño 1962, in the California Current off California and Baja California. *Anales del Instituto de Ciencias del Mar y Limnología*. Universidad Nacional Autónoma de México, 10 (1):47-84.

---------- 1983b. *Nectocarmen antonioi*, a new Prayinae, Calycophorae, Siphonophora, from California. *Proceedings of the Biological Society of Washington*, 96(3):339-348.

---------- 1985. Distribución batimétrica de especies del Género *Lensia* en aguas de California y Baja California (Diphyinae, Siphonophora, Coelenterata). *Investigaciones Marinas CICIMAR*, 2(1):59-80.

ALVARIÑO, A., J.M. WOJTAN & M.R. MARTINEZ, 1990. Antarctic Siphonophora from plankton samples of the United States Antarctic Research Program, ELTANIN Cruises 3-5, 8-23, 25-28, 30, 35, 38. American Geophysical Union, Antarctic Series, Kornicker Editor Vol. 49:1-436.

BARHAM, E.G., 1963. Siphonophores and the Deep scattering layer. *Science*, 140 (3568):826-828.

---------- 1966. Deep scattering layer migrations and composition. Observations from a Diving Saucer. *Science* 1951 (3716):1399-1403.

BIGELOW, H.B., 1911. Report on the scientific results of the Expedition to the Eastern tropical Pacific 1904-1905. XXIII. The Siphonophorae Memoirs of the Museum of Comparative Zoology, 38:171-402.

BIGELOW, H.B. & M. LESLIE, 1930. Reconnaisance of the waters of plankton of Monterey Bay, 1928. *Bulletin of the Museum of Comparative Zoology Harvard College*, 70:429-581.

BIGGS, D.C., 1977. Field studies of fishing, feeding and digestion in Siphonophores. *Marine Behavior and Physiology*, 4(4):261-274.

BIGGS, D.C., R.R. BIDIGARE & D.E. SMITH, 1981. Population density of gelatinous macrozooplankton; *in situ* estimation in oceanic surface waters. *Biological Oceanography*, 1(2):157-173.

HAMNER, W.N., L.P. MADIN, A.L. ALLDREDGE, R.W. GILMER & P.O. HAMNER, 1975. Underwater observations of gelatinous zooplankton: Sampling problems, feeding biology, and behavior. *Limnology and Oceanography*, 29(6):907-917.

PUGH, P.R., 1974. The vertical distribution of the Siphonophores collected during the SOND Cruise, 1965. *Journal of the Marine Biological Association of the United of Kingdom*, 54(1):25-90.

---------- 1977. Some observations on the vertical migration and geographic distribution of Siphonophores in the warm waters of the North Atlantic Ocean. Proceedings Symposium of Warm Water Zoology:362-378.

SEARS, M., 1963. Notes on Siphonophores. 2. A revision of the Abylinae. *Bulletin of the Museum of Comparative Zoology*, Harvard College, 109(1):1-119.

TOTTON, A.K., 1965. A new species of *Lensia* (Siphonophora, Diphyidae) from the coastal waters of Vancouver, B.C. *Annales Magazine Natural History*, Serie 13, 8(86);71-76.

TOTTON, A.K. & H.E. BARGMANN, 1965. *A Synopsis of the Siphonophora*. British Museum Natural History.230 pp.

TABLA 1. DATOS NUMERICOS NORMALIZADOS SOBRE LA DISTRIBUCION DE ESPECIES DE SIFONOFOROS. (p = Fase poligástrica. e = Fase eudoxia).

Crucero	Estación	Fecha	Hora	Prof. (m)	Abundancia
FAMILIA: EPIBULIDAE *Epibulia ritteriana* Haeckel, 1888					
6902-03	90.45	11-III-69	1005	25-15	2
			2206	15-0	2
6908-09	70.90	18-VIII-69	0030	50-25	1
	90.45	03-IX-69	1255	25-0	1
				50-25	2
		04-IX-69	0054	25-0	1
	90.60	05-IX-69	1205	50-25	1
			0015	50-25	1
FAMILIA APOLEMIIDAE *Apolemia uvaria* (Lesueur, 1811)					
6902-03	90.60	10-III-69	1115	22-11	1
				75-50	1
		11-III-69	0035	100-75	18
FAMILIA AGALMIDAE *Agalma okeni* Eschscholtz, 1825					
6902-03	90.45	11-III-69	2206	25-15	9 larvas
	90.60	10-III-69	1115	11-0	1
	120.55	05-III-69	2126	15-0	1
				25-15	1
				50-25	1
				75-50	1
		06-III-69	0112	100-75	2
	120.70		2240	15-0	1
				25-15	1
				50-25	1
				75-50	1
	120.90	07-III-69	2150	15-0	2
				25-15	4 larvas
				50-25	2
				75-50	2
		08-III-69	1019	100-75	1
			1247	300-250	1
6905-06	70.90	17-V-69	1343	225-100	40 larvas
	90.60	27-V-69	2200	50-25	1
				75-50	100 larvas
		28-V-69	0947	50-25	5 larvas
	90.90	07-V-69	2355	25-0	1
				75-50	1
	120.45	22-VI-69	2100	25-0	1
				100-75	1
	120.55	22-VI-69	2135	50-25	1
	120.90	20-VI-69	1215	475-350	1
			2100	50-25	1
				75-50	1

Crucero	Estación	Fecha	Hora	Prof. (m)	Abundancia
6908-09	70.60	15-VIII-69	1000	475-350	5 larvas
	120.70	28-IX-69	0050	50-25	1
				75-50	1
6911-12	120.70	08-XII-69	1000	50-25	1
				75-50	1
			2140	25-0	1
	120.90	09-XII-69	2135	25-0	2
				75-50	1

Stephanomia bijuga (delle Chiaje, 1841, 1842)

6902-03	70.60	22-II-69	0000	50-25	7 larvas
			1249	75-50	1
			1632	208-160	1
	70.75	23-II-69	2230	15-0	1
				25-15	1
	90.60	10-III-69	1115	50-34	50 larvas
			1348	100-75	1
	120.90	07-III-69	2240	25-15	1
6905-06	70.60	21-V-69	2220	50-25	29 larvas
		22-V-69	1006	75-50	13 larvas
	70.75	20-V-69	2155	50-25	17 larvas
				75-50	3
				100-75	1
		21-V-69	0953	50-25	1
			1245	475-350	1
	70.90	20-V-69	0053	350-225	5
	90.45	29-V-69	0115	225-100	1
	90.60	27-V-69	2200	25-0	18 larvas
				100-75	8 larvas
		28-V-69	0947	75-50	1
				100-75	2
	120.55	22-VI-69	2300	225-100	1
6908-09	70.60	15-VIII-69	1000	225-100	10 larvas
				350-225	2
	70.75	16-VIII-69	1030	225-100	5 larvas
				350-225	10 larvas
		17-VIII-69	0300	75-50	10 larvas
		16-VIII-69	2140	225-100	80 larvas
				475-350	5 larvas
6908-09	70.90	17-VIII-69	2125	350-225	30 larvas
		18-VIII-69	0930	225-100	60 larvas
				350-225	30 larvas
			1215	50-25	2
	70.110	19-VIII-69	2120	225-100	1
				350-225	10 larvas
	90.45	03-IX-69	1255	75-50	1
				100-75	1
			1010	475-350	45 larvas
			2200	225-100	40 larvas
				475-350	5 larvas
		04-IX-69	0054	100-75	6 larvas
	90.60	04-IX-69	2130	225-100	15 larvas
				475-350	22 larvas
		05-IX-69	0015	100-75	4 larvas
			0930	475-350	3

Crucero	Estación	Fecha	Hora	Prof. (m)	Abundancia
6911-12	70.60	20-XI-69	1030	50-25	1
			1258	475-350	1
			2345	25-0	1
				50-25	1
				75-50	1
			2135	225-100	5 larvas
				350-225	5 larvas
				475-350	5 larvas
				600-475	10 larvas
	70.75	21-XI-69	0930	225-100	2
				350-225	1
	90.45	03-XII-69	0010	225-100	1
	120.90	09-XII-69	2325	225-100	1
Stephanomia rubra Vogt, 1852					
6911-12	90.90	14-XII-69	1145	475-350	1
Agalma elegans Fewkes, 1880 (Sars, 1846)					
6905-06	70.90	19-V-69	1215	100-75	1
Erenna richardi Bedot, 1904					
6908-09	70.90	18-VIII-69	1215	75-50	1
Nanomia cara A. Agassiz 1865					
6908-09	90.90	06-IX-69	0930	600-475	1
Moseria convoluta (Moser, 1925)					
6911-12	90.60	13-XII-69	1235	350-225	1
FAMILIA: PYROSTEPHIDAE					
Bargmannia elongata Totton, 1954					
6905-06	70.60	22-V-69	1318	475-350	5
	90.45	29-V-69	0115	225-100	10
6908-09	70.90	18-VIII-69	0930	350-225	5
	70.75	16-VIII-69	2140	350-225	110
	90.90	06-IX-69	2120	600-475	9
	120.70	27-IX-69	2116	475-350	70
Physophora hydrostatica Forskål, 1775					
6902-03	70.75	23-II-69	1045	75-50	1
	90.45	11-III-69	1005	15-0	1
				40-25	1
				50-40	1
			1214	130-95	10
			2206	50-40	1
			2304	130-95	1
	90.60	10-III-69	2313	11-0	1
				22-11	1
				75-50	1
		11-III-69	0035	100-75	1
	120.70	06-III-69	2240	50-25	1

Crucero	Estación	Fecha	Hora	Prof. (m)	Abundancia
6905-06	70.60	21-V-69	2220	100-75	1
	90.60	28-V-69	0947	75-50	1
6908-09	70.75	16-VIII-69	2140	350-225	1
	70.90	18-VIII-69	0930	225-100	1
			1215	100-75	36
	70.110	19-VIII-69	2120	225-100	1
	90.90	06-IX-69	2336	25-0	1
				100-75	1
6911-12	70.60	20-XI-69	1258	600-475	5
			2135	600-475	5
			2345	25-0	1
	90.45	08-XII-69	2130	25-0	3
				75-50	1
	120.90	09-XII-69	2135	50-25	1

FAMILIA: ATHORYBIIDAE

Athorybia rosacea (Forskål, 1775)

6908-09	90.90	06-IX-69	2336	50-25	7

FAMILIA: FORSKALIIDAE

Forskalia edwardsi Kölliker, 1853

6905-06	90.60	28-V-69	1256	475-350	1
				600-475	1

FAMILIA: PRAYIDAE, SUB-FAMILIA: AMPHICARYONINAE

Amphicaryon acaule Chun, 1888

6905-06	70.60	21-V-69	2220	50-25	1
	70.75	20-V-69	2155	50-25	1
	70.90	19-V-69	1215	75-50	1
		20-V-69	0053	350-255	45
	70.110	17-V-69	1343	225-100	5
6908-09	70.110	19-VIII-69	1230	100-75	2
			2325	75-50	1
				100-75	1
	90.60	05-IX-69	0015	50-25	2
			1205	50-25	3
				75-50	1
	90.90	06-IX-69	0930	225-100	20
			2120	225-100	5
			2336	100-75	3
	120.55	26-IX-69	2115	225-100	10
		27-IX-69	0013	100-75	10
	120.90	28-IX-69	2130	475-350	5
6911-12	90.60	12-XII-69	2130	75-50	1
		13-XII-69	0930	50-25	1
				75-50	2
	90.90	14-XII-69	0930	100-75	1

Crucero	Estación	Fecha	Hora	Prof. (m)	Abundancia
Amphicaryon ernesti Totton, 1954					
6905-06	70.60	22-V-69	1006	75-50	2
6908-09	70.110	19-VIII-60	1000	475-350	5
			2120	225-100	65
	90.60	05-IX-60	0015	75-50	2
			0930	350-225	5
	90.90	06-IX-69	0930	225-100	5
			2336	75-50	1
6911-12	70.60	20-XI-69	1030	75-50	1
				100-75	1
	90.90	14-XII-69	0930	50-25	1
FAMILIA: PRAYIDAE, SUB-FAMILIA: PRAYINAE *Rosacea plicata* Quoy & Gaimard, 1827					
6905-06	70.60	21-V-69	0020	350-225	1
	70.75	20-V-69	2353	475-350	1
	90.60	28-V-60	0947	50-25	1
	90.90	07-V-69	2355	25-0	1
6908-09	70.90	17-VIII-69	2125	475-350	5
		18-VIII-69	1215	75-50	1
	70.110	19-VIII-69	1230	475-350	5
	90.60	05-IX-60	0930	475-350	5 y 5 larvas
	120.55	27-IX-69	0932	475-350	5 larvas
	120.90	27-IX-69	2116	475-350	15
		28-IX-69	2130	350-225	5
		29-IX-69	0915	350-225	10
Rosacea cymbiformis (delle Chiaje, 1822)					
6905-06	70.75	21-V-69	0953	25-0	1
6908-09	120.70	28-IX-69	0915	475-350	10 p, 5e
6911-12	120.70	08-XII-69	1222	475-350	1
Nectodroma dubia (Quoy & Gaimard, 1833, 1834)					
6905-06	70.75	21-V-69	0953	100-75	1
	70.110	17-V-69	2217	50-25	1
6908-09	70.110	19-VIII-69	2325	25-0	1
	120.55	27-IX-69	0932	350-225	1
6911-12	70.75	21-XI-69	0930	475-350	1
	90.45	03-XII-69	0010	225-100	1
FAMILIA: PRAYIDAE, SUB-FAMILIA: PRAYINAE *Nectodroma reticulata* Bigelow, 1911					
6902-03	70.75	23-II-69	1045	75-50	1
			1619	350-225	1
	90.45	11-III-69	1005	60-50	1
6908-08	70.90	18-VIII-69	0040	50-25	1
	90.60	05-IX-69	0939	475-350	2
	120.45	25-IX-69	2120	225-100	1

Crucero	Estación	Fecha	Hora	Prof. (m)	Abundancia
6911-12	120.70	08-XII-69	2325	350-225	2
Desmophyes annectens Haeckel, 1888					
6902-03	90.45	11-II-69	2304	168-130	1
6905-06	70.75	21-V-69	1245	600-475	1
Nectocarmen antonioi Alvariño, 1983					
6905-06	90.60	28-V-69	0947	75-50	1
FAMILIA: PRAYIDAE, SUB-FAMILIA: NECTOPYRAMIDINAE *Nectopyramis dioimedeae* Bigelow, 1911					
6905-06	70.75	20-V-69	2352	600-475	1
	120.90	20-VI-69	1215	475-350	5
6908-09	70.110	19-VIII-69	2120	475-350	1
6911-12	70.75	21-XI-69	0930	475-350	1
	120.70	8-XII-69	2335	600-475	1
Nectopyramis natans (Bigelow, 1911)					
6908-09	120.90	29-IX-69	0915	475-350	5
Nectopyramis spinosa Sears, 1952					
6905-06	70.110	18-V-69	0140	475-350	1
Nectopyramis thetis Bigelow, 1911					
6905-06	70.75	20-V-69	2353	350-225	1
FAMILIA: HIPPOPODIIDAE *Hippopodius hippopus* (Forskal, 1776)					
6902-03	90.45	11-II-69	2304	130-95	1
	90.60	10-III-69	1348	100-75	2
6905-06	90.60	28-V-69	0947	75-50	1
				100-75	1
	90.90	07-V-69	2355	50-25	1
6908-09	70.110	19-VIII-69	1000	350-225	1
			2325	25-0	1
	90.90	06-IX-69	1220	75-50	1
	120.70	28-IX-69	1129	75-50	1
6911-12	90.45	02-XII-69	0939	50-25	1
		08-XII-69	2130	25-0	1
	90.60	13-XII-69	0930	75-50	1
	90.90	14-XII-69	0930	50-25	1
			2135	25-0	1

Crucero	Estación	Fecha	Hora	Prof. (m)	Abundancia
Vogtia kuruae Alvariño, 1967					
6905-06	70.90	19-V-69	1436	475-350	13
				600-475	1
		20-V-69		600-475	5
	90.45	29-V-69	0115	475-350	6
	120.55	22-VI-69	2300	475-350	1
6908-09	70.75	16-VIII-69	1030	350-225	2
			2140	350-225	1
	70.90	17-VIII-69	2125	350-225	2
		18-VIII-69	0930	350-225	2
	70.110	19-VIII-69	1000	475-350	1
			2120	350-225	6
				475-350	2
	90.45	03-IX-69	1010	475-350	2
			2200	475-350	2
	120.55	27-IX-69	0932	475-350	2
	120.70	28-IX-69	0915	475-350	2
6911-12	70.75	21-XI-69	0939	350-225	1
	90.60	12-XII-69	2355	475-350	1
	120.55	07-XII-69	2145	25-0	1
			2355	475-350	1
	120.90	09-XII-69	2325	475-350	4
		10-XII-69	1200	475-350	2
Vogtia pentacantha Kölliker, 1853					
6902-03	70.75	23-II-69	1619	350-225	1
6908-09	70.90	17-VIII-69	2125	475-350	1
6911-12	70.60	20-XI-69	1258	600-475	5
	90.90	14-XII-69	1145	475-350	1
Vogtia serrata (Moser, 1925)					
6905-06	70.75	21-V-69	1245	600-475	5
6908-09	120.90	29-IX-69	0915	600-475	1
6911-12	70.75	21-XI-69	0930	600-475	6
Vogtia spinosa Keferstein & Ehlers, 1861					
6902-03	70.75	23-II-69	1619	350-225	1
6905-06	70.110	17-V-69	1343	475-350	4
6911-12	70.60	20-XI-69	2135	225-100	5
FAMILIA: DIPHYIDAE, SUB-FAMILIA: SULCULEOLARIINAE *Sulculeolaria biloba* (Sars, 1846)					
6908-09	70.110	19-VIII-69	2325	75-50	1 p
Sulculeolaria chuni (Lens & van Riemsdijk, 1908)					
6908-09	120.70	28-IX-69	0050	25-0	1 p

Crucero	Estación	Fecha	Hora	Prof. (m)	Abundancia
Sulculeolaria monoica (Chun, 1888)					
6902-03	120.90	08-III-69	1247	250-200	1 p
6905-06	90.60	27-V-69	2200	50-25	4 p
	90.90	07-V-69	2355	50-25	1 p
6908-09	70.110	19-VIII-69	2325	25-0	7 p
				75-50	2 p
	90.90	06-IX-69	1220	50-25	3 p
			2336	25-0	35 p
	120.70	28-IX-69	0050	25-0	1 p
				50-25	1 p
6911-12	90.60	12-XII-69	2130	50-25	2 p
		13-XII-69	0930	50-25	1 p
	90.90	14-XII-69	0930	25-0	1 p
				100-75	1 p
			2135	25-0	3 p
	120.90	09-XII-69	2135	25-0	1 p
				50-25	1 p
Sulculeolaria quadrivalvis Blainville, 1834					
6902-03	70.60	22-II-69	0000	50-25	1 p
	90.60	10-III-69	2313	34-22	1 p
	120.70	07-III-69	0955	15-0	11 p
	120.90	07-III-69	2240	25-25	1 p
		08-III-69	0010	100-75	1 p
			1019	50-25	3 p
			1247	150-100	4 p
6905-06	70.60	22-V-69	1006	25-0	1 p
	70.75	20-V-69	2155	25-0	1 p
		21-V-69	0953	50-25	1 p
	70.90	19-V-69	1215	50-25	1 p
	90.60	27-V-69	2200	25-0	19 p
	90.90	07-V-69	2355	25-0	1 p
				50-25	1 p
		08-V-69	1105	25-0	2 p
				50-25	1 p
	120.45	23-VI-69	0910	100-75	1 p
6908-09	70.90	18-VIII-69	1215	50-25	2 p
				75-50	1 p
	70.110	19-VIII-69	1000	350-225	30 p
6911-12	90.60	12-XII-69	2130	25-0	1 p
	90.90	14-XII-69	1145	225-100	5 p
	120.70	08-XII-69	2325	475-350	75 p
FAMILIA: DIPHYIDAE, SUB-FAMILIA: DIPHYINAE *Chelophyes contorta* (Lens & van Riemsdijk, 1908)					
6902-03	120.70	06-III-69	2240	15-0	24 p
				25-15	37 p
				50-25	17 p
		07-III-69	0955	15-0	9 p
				50-25	1 p
				75-50	4 p

Crucero	Estación	Fecha	Hora	Prof. (m)	Abundancia
		Dimophyes arctica (Chun, 1897)			
6902-03	90.60	10-II-69	1439	176-100	3 p
6908-09	70.110	19-III-69	1000	475-350	10 p
		Diphyes bojani (Eschscholtz, 1829)			
6902-03	70.75	23-II-69	1045	50-25	1 p
	120.90	07-III-69	2240	50-25	1 p
		08-III-69	1019	50-25	8 p
6905-06	70.90	19-V-69	1215	50-25	1 p
	70.110	17-V-69	2217	50-25	24 e
				100-75	10 e
	90.90	07-V-69	2355	25-0	168 p,135 e
				100-75	16 e
		08-V-69	1105	75-50	256 e
6908-09	70.110	19-VIII-69	2325	25-0	9 p
	90.60	05-IX-69	1205	50-25	45 e
	90.90	06-IX-69	1220	50-25	2 p, 2 e
				75-50	15 e
			2336	25-0	1 p
				50-25	1 p, 30 e
6911-12	90.90	14-XII-69	0930	25-0	200 p,60 e
				50-25	531 p,153 e
				70-50	33 p
				100-75	3 p
			1145	225-100	305 p,380 e
			2135	25-0	78 p
	120.90	10-XII-69	0949	50-25	19 p
		Diphyes dispar Chamisso & Eysenhardt, 1821			
6902-03	70.60	22-II-69	0000	25-0	1 p
	70.75	23-II-69	1045	25-15	17 p
	120.45	05-III-69	1215	25-15	2 p
	120.90	07-III-69	2150	15-0	1 p
			2240	25-15	2 p
				50-25	1 p
		08-III-69	0010	100-75	106 p,213 e
6905-06	90.90	07-V-69	2355	50-25	1 p
				75-50	1 p
		08-VI-69	1105	50-25	1 p, 403 e
	120.45	22-VI-69	2100	25-0	2 p
6908-09	90.60	05-IX-69	0015	25-0	1 p, 15 e
	90.90	06-IX-69	1220	25-0	1 p
				50-25	1 p
			2336	25-0	2 p, 2 e
				50-25	1 p
	120.55	26-IX-69	2115	350-225	80 p
		27-IX-69	0013	100-75	30 p
			1201	25-0	47 p, 15 e
	120.70	28-IX-69	0050	25-0	31 p
				50-25	1 p, 1 e
	120.90	29-IX-69	1200	25-0	15 p

Crucero	Estación	Fecha	Hora	Prof. (m)	Abundancia
6911-12	70.60	20-XI-69	1040	25-0	68 p,822 e
				100-75	1 e
			2345	25-0	2 p
				100-75	3 p, 1 e
	90.45	02-XII-69	0939	50-25	2 p, 2 e
				75-50	3 p, 15 e
		03-XII-69	0010	225-100	5 p, 5 e
		08-XII-69	2130	25-0	11 p, 1 e
				75-50	3 p
				100-75	6 p
	90.60	12-XII-69	2130	25-0	13 p, 16 e
				50-25	3 p, 361 e
		13-XII-69	0930	25-0	4 p, 5 e
	90.90	14-XII-69	0930	25-0	47 p, 50 e
				100-75	30 e
			2135	25-0	1 p, 30 e
6911-12	120.55	07-XII-69	0935	25-0	180 e
			1220	225-100	15 e
			2145	50-25	1 p
	120.70	08-XII-69	1000	25-0	1 p, 125 e
			2140	25-0	61 e
				50-25	1 p, 61 e
				100-75	2 p
			2325	225-100	10 p,150 e
	120.90	09-XII-69	2135	25-0	49 p, 46 e
				50-25	22 p, 31 e
		10-XII-69	0940	25-0	27 p
				50-25	8 p

Diphyopsis mitra (Huxley, 1859)

6902-03	90.60	10-III-69	1115	75-50	16 e
			1348	100-75	17 e
	120.70	06-III-69	2240	25-15	103 p,42 e
				50-25	34 p, 8 e
		07-III-69	0955	25-15	33 e
	120.90	08-III-69	1247	150-100	42 e
6905-06	70.90	19-V-69	1215	100-75	9 e
	70.110	17-V-69	2217	50-25	16 e
				100-75	68 p
	120.55	22-VI-69	0910	50-25	8 e
6908-09	70.110	19-VIII-69	1000	350-225	5 e
			2120	350-225	128 e

FAMILIA: CLAUSOPHYIDAE

Chuniphyes multidentata Lerns & van Riemskijk, 1908

Crucero	Estación	Fecha	Hora	Prof. (m)	Abundancia
6902-03	90.45	11-II-69	2304	168-130	10 p
6905-06	70.60	22-V-69	0020	225-100	5 p
				350-225	95 p
				475-350	70 p
				600-475	10 p
			1318	475-350	130 p
				600-475	10 p
	70.75	20-V-69	2353	225-100	115 p
				350-225	115 p
				475-350	285 p
				600-475	170 p
		21-V-69	1245	475-350	90 p
				600-475	105 p,20 e
	70.90	19-V-69	1436	350-225	10 p
				475-350	345 p
				600-475	10 p
		20-V-69	0053	350-225	225 p
				475-350	100 p
				600-475	20 p
	70.110	17-V-69	0140	350-225	5 p
				475-350	25 p
				600-475	5 p
	90.45	29-V-69	0115	350-225	195 p
				475-350	75 p, 75 e
				600-475	25 p
	90.60	28-V-69	0032	475-350	20 p
				600-475	10 p
			1256	475-350	85 p
				600-475	10 p
	90.90	8-0V-69	0244	475-350	5 p
				600-475	245 p
	120.45	23-VI-69	2330	475-350	5 e
	120.55	22-VI-69	1210	350-225	50 p
				475-350	30 p
				600-475	20 p
			2300	475-350	20 p
	120.70	21-VI-69	1230	600-475	30 p, 20 e
			2310	475-350	5 p
				600-475	5 p
6908-09	70.60	15-VIII-69	1000	475-350	10 p
				600-475	10 p
	70.75	16-VIII-69	1030	225-100	20 p
				475-350	10 p
			2140	350-225	25 p
				475-350	15 p
	70.90	17-VIII-69	2125	350-225	60 p
				475-350	35 p
		18-VIII-69	0930	475-350	15 p, 10 e
	70.110	19-VIII-69	1000	475-350	25 p, 10 e
			2120	350-225	10 p
				475-350	70 p, 20 e
	90.45	03-IX-69	1010	475-350	70 p
			2200	600-475	20 e
	90.60	05-IX-69	0930	475-350	85 p
				600-475	20 p
	90.90	06-IX-69	0930	475-350	40 p
			2120	475-350	25 p

Crucero	Estación	Fecha	Hora	Prof. (m)	Abundancia
				600-475	5 p
	120.45	25-IX-69	2120	600-475	5 p
		26-IX-69	0955	475-350	5 p, 5 e
				600-475	5 p
	120.55	26-IX-69	2115	475-350	5 p, 5 e
				600-475	20 p
		27-IX-69	0932	350-225	15 p
				475-350	25 p
				600-475	5 p, 5 e
	120.70	27-IX-69	2116	600-475	5 p
		28-IX-69	0915	475-350	5 p
				600-475	5 p
	120.90	29-IX-69	0915	600-475	10 p, 5 e
			2130	600-475	5 p, 5 e
6911-12	70.60	20-XI-69	1258	350-225	10 p
				475-350	90 p
				600-475	310 p
			2135	475-350	20 p
				600-475	120 p
	70.75	21-XI-69	0930	350-225	10 p
				475-350	30 p
				600-475	10 p, 25 e
6911-12	90.60	12-XII-69	2355	600-475	150 p
		13-XII-69	1235	350-225	75 p, 5 e
	90.90	14-XII-69	1145	475-350	65 p
	120.45	05-XII-69	2345	475-350	25 p
		06-XII-69	1230	475-350	5 p
				600-475	10 p
	120.90	09-XII-69	2325	475-350	5 p
				600-475	10 p

Clausophyes ovata (Keferstein & Ehlers, 1860)

Crucero	Estación	Fecha	Hora	Prof. (m)	Abundancia
6905-06	70.60	22-V-69	0020	600-475	10 p
			1318	475-350	5 p
				600-475	65 p
	70.75	20-V-69	2353	475-350	5 p
				600-475	10 p
		21-V-69	1245	600-475	20 p
	70.90	19-V-69	1436	475-350	40 p
				600-475	25 p
		20-V-69	0053	475-350	20 p
				600-475	5 p
	70.110	18-V-69	1040	600-475	15 p
	90.45	29-V-69	0115	475-350	10 p
				600-475	15 p
	90.60	28-V-69	0032	600-475	10 p
			1256	600-475	5 p
	120.55	22-VI-69	1210	600-475	5 p
	120.70	21-VI-69	1230	600-475	10 p
			2310	475-350	5 p

Crucero	Estación	Fecha	Hora	Prof. (m)	Abundancia
6908-09	70.90	17-VIII-69	2125	475-350	5 p
		18-VIII-69	0930	475-350	10 p
	70.110	19-VIII-69	2120	475-350	20 p
	90.45	03-IX-69	1010	475-350	5 p
				600-475	10 p
	90.60	04-IX-69	2130	350-225	5 e
				475-350	30 p, 10 e
				600-475	80 p
		05-IX-69	0930	600-475	60 p
	120.45	25-IX-69	2120	475-350	5 p, 5 e
		26-IX-69	0955	600-475	5 p
	120.55	26-IX-69	2115	600-475	10 p
		27-IX-69	0932	600-475	20 p
	120.70	27-IX-69	2116	600-475	10 p
		28-IX-69	0915	600-475	20 p
	120.90	28-IX-69	2130	600-475	40 p
6911-12	70.60	20-XI-69	1258	600-475	40 p
	70.75	21-XI-69	0930	475-350	5 p
				600-475	15 p
	90.60	12-XII-69	2355	475-350	85 p
				600-475	5 p
		13-XII-69	1235	350-225	5 p
				475-350	10 p
	120.55	07-XII-69	2355	475-350	5 p
	120.70	08-XII-69	1222	600-475	10 p
			2325	600-475	5 p
	120.90	09-XII-69	2325	600-475	40 p

FAMILIA: SPHAERONECTIDAE

Sphaeronectes gracilis (Claus, 1873, 1874)

6902-03	90.45	11-III-69	1005	25-15	3385
				40-25	510
			2206	40-25	36
	90.60	10-III-69	1115	34-22	125
				50-34	348
				75-50	303
			1348	100-75	298
			2313	11-0	16
6905-06	90.45	28-V-69	2253	25-0	740
				50-25	20
				75-50	33
				100-75	76
	120.70	21-VI-69	2115	100-75	1

FAMILIA: ABYLIDAE, SUB-FAMILIA: ABYLINAE

Abyla haeckeli Lens & van Riemsdijk, 1908

6902-03	90.60	10-III-69	1115	11-0	17 e
				75-50	1 e
6905-06	90.60	27-V-69	2200	75-50	1 e
		28-V-69	0947	50-25	1 e

Crucero	Estación	Fecha	Hora	Prof. (m)	Abundancia
6908-09	90.60	05-IX-69	0015	25-0	1 e
			1205	25-0	4 e
				50-25	4 e
				75-50	2 e
	90.90	06-IX-69	1220	50-25	5 e
			2336	25-0	2 e
				50-25	5 e
6911-12	90.45	02-XII-69	0930	50-25	2
		08-XII-69	2130	25-0	1 e
	90.90	14-XII-69	0930	25-0	31 e
	120.90	09-XII-69	2135	50-25	1 e
Abyla bicarinata Moser, 1925					
6905-06	90.60	27-V-69	2200	50-25	1 p
6908-09	90.90	06-IX-69	2336	50-25	3 p
6911-12	90.45	02-XII-69	2130	25-0	1 p
Abyla brownia Sears, 1953					
6902-03	90.60	10-III-69	1115	50-34	1 p
FAMILIA: ABYLIDAE, SUB-FAMILIA: ABYLOPSINAE					
Abylopsis eschscholtzi (Huxley, 1859)					
6909-09	90.90	06-IX-69	1220	50-25	1 p
			2336	75-50	15 p
Abylopsis tetragona (Otto, 1823)					
6902-03	120.90	07-III-69	2150	15-0	1 p
		08-III-69	1019	50-25	1 p
			1247	150-100	42 p
6905-06	90.90	07-V-69	2355	25-0	8 p, 50 e
6908-09	90.90	06-IX-69	2336	25-0	1 e
				50-25	1 e
6911-12	90.90	14-XII-69	0930	25-0	61 p, 46 e
				50-25	47 p,160 e
				100-75	1 p, 15 e
			1145	475-350	5 p
Bassia bassensis (Quoy & Gaimard, 1833, 1834)					
6905-06	90.90	07-V-69	2355	25-0	8 p
6908-09	70.110	19-VIII-69	2325	25-0	1 p
	90.90	06-IX-69	1220	50-25	1 p
	120.70	28-IX-69	1129	75-50	15 p
6911-12	90.90	14-XII-69	0930	50-25	1 p
Enneagonum hyalinum Quoy & Gaymanrd, 1827					
6905-06	120.90	20-VI-69	0930	25-0	1 p
6908-09	120.90	29-IX-69	1200	25-0	2 p

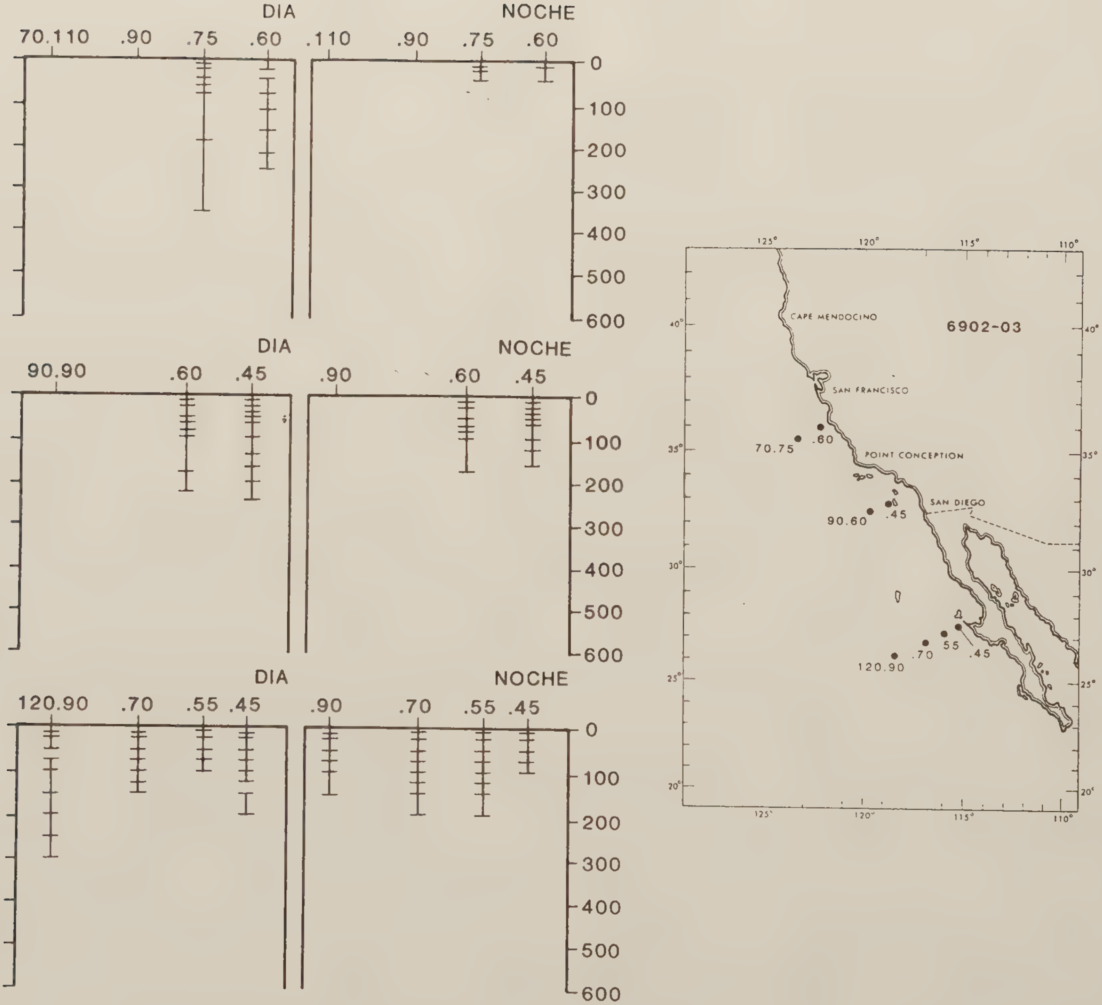

Figura 1 a. Distribución de las Estaciones y arrastres batimétricos efectuados en el invierno, durante el día y la noche. Los segmentos verticales indican los arrastres realizados. Mapa tomado de Alvariño, 1983a).

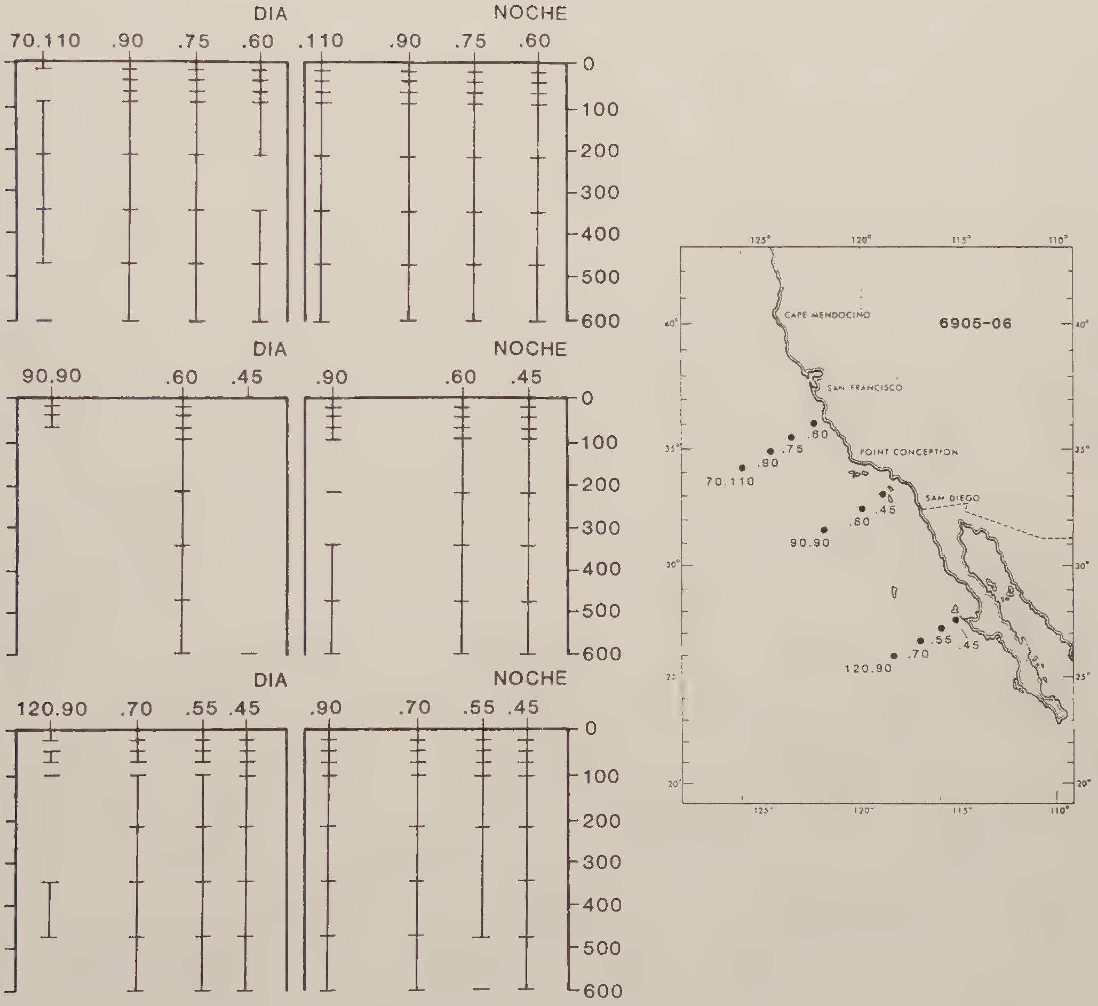

Figura 1 b. Distribución de las Estaciones y arrastres batimétricos efectuados en la primavera, durante el día y la noche. Los segmentos verticales indican los arrastres realizados. (Mapa tomado de Alvariño, 1983a).

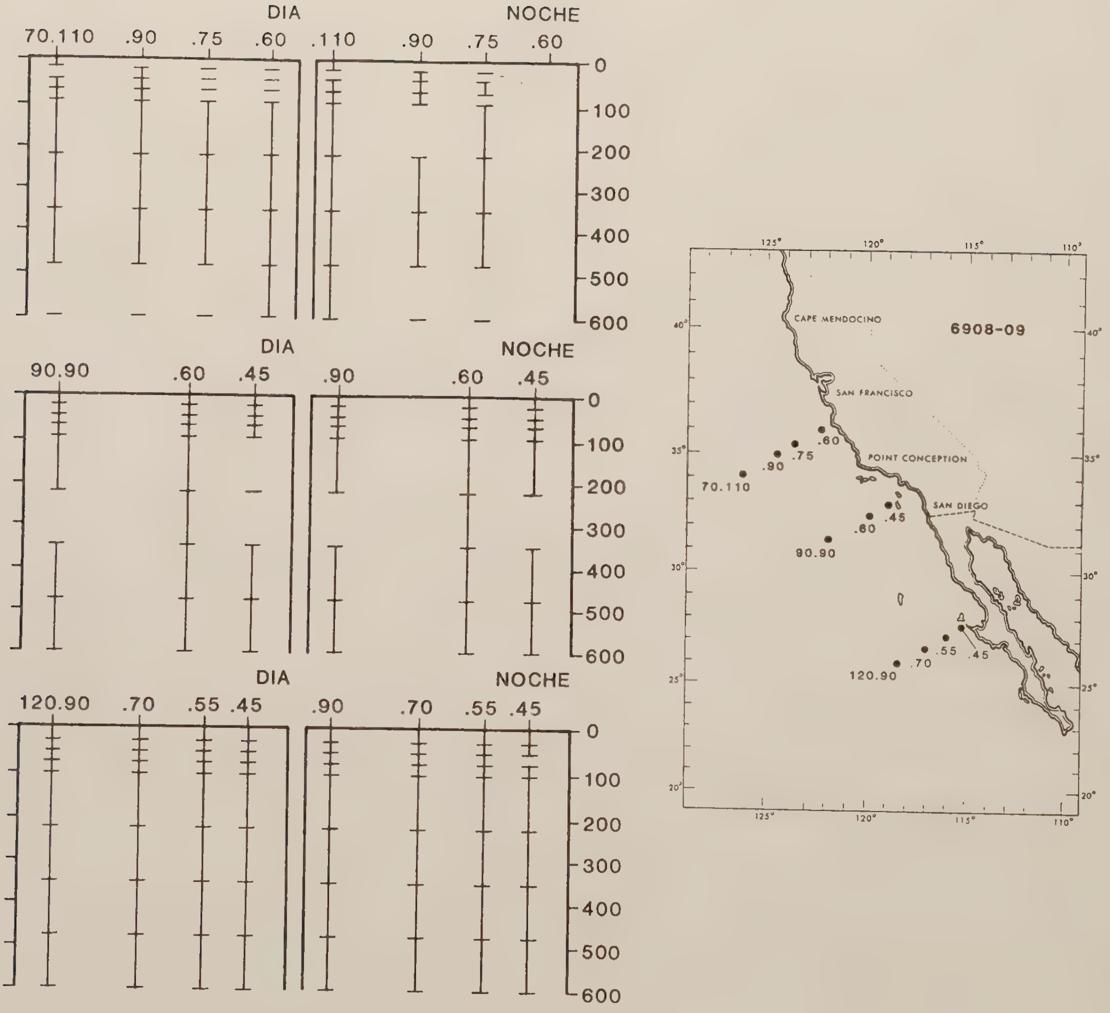

Figura 1 c. Distribución de las Estaciones y arrastres batimétricos efectuados en el verano, durante el día y la noche. Los segmentos verticales indican los arrastres realizados. (Mapa tomado de Alvariño, 1983a).

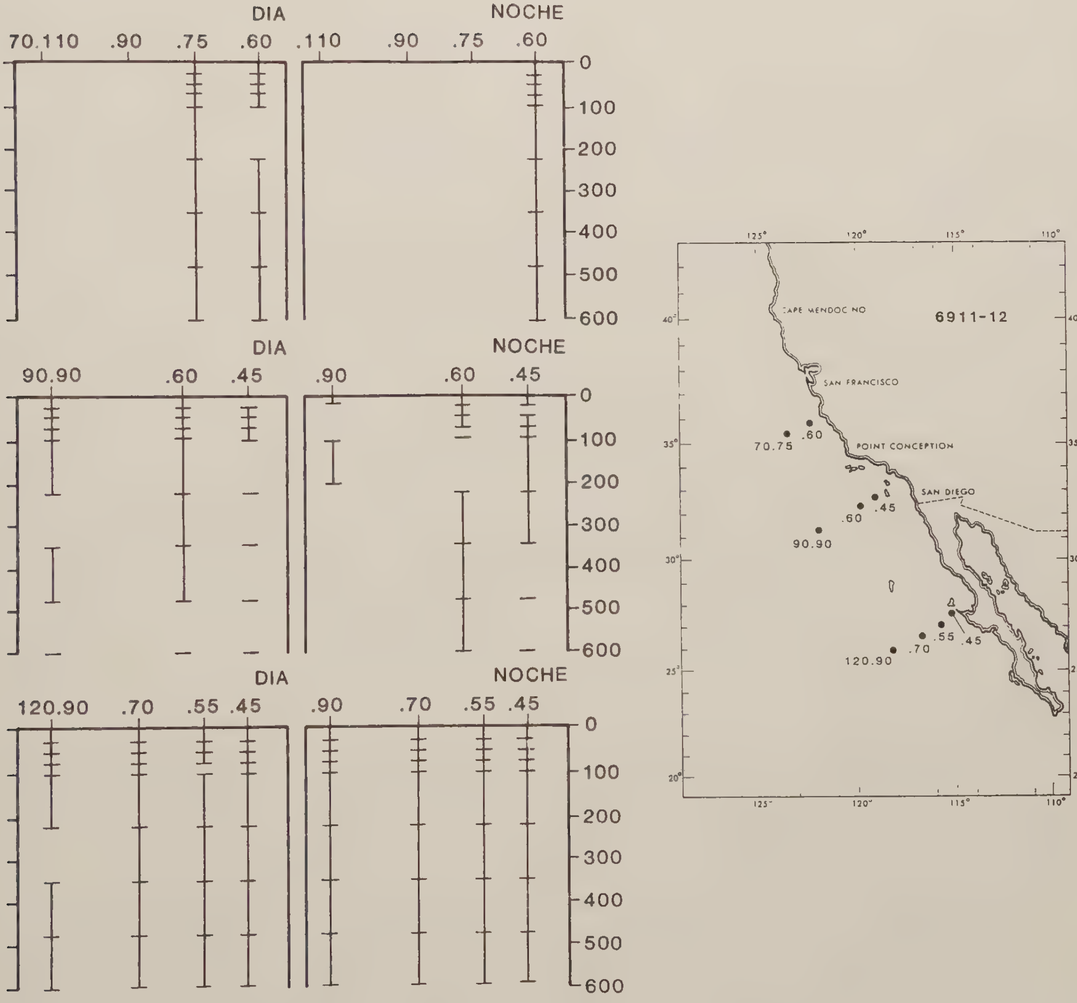

Figura 1 d. Distribución de las Estaciones y arrastres batimétricos efectuados en el otoño, durante el día y la noche. Los segmentos verticales indican los arrastres realizados. (Mapa tomado de Alvariño, 1983a).

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8. CHAETOGNATHA

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I. INTRODUCTION

Asexual propagation does not occur in chaetognaths. When a chaetognath is broken, regeneration occurs only of the part that includes the head and the ventral ganglion. If the head is missing, the ventral ganglion assumes the direction of the regenerative process. However, there is no production of other individuals, only a regeneration of the missing part of the animal.

II. REGENERATION

Few experiments have been conducted on regeneration in chaetognaths. Kulmatycki (1918) and Ghirardelli (1968) found that *Spadella cephaloptera* could regenerate the whole caudal section, and *Sagitta helenae* and *S. enflata* the head (Pierce, 1951).

In animals there appears to be a close correlation between regenerative power and the stage at which segregation of the germinal line occurs (Ghirardelli, 1968). Animals with precocious determination of the primordial germ cell have usually limited regenerative ability, insufficient for the reconstruction of complete new individuals from a portion of the body, and they cannot regenerate important and large portions of the body. They also lack the power of asexual reproduction by fission or budding (Ghirardelli, 1956, 1959a). In Chaetognatha, segregation of the germinal-line determinant occurs early in development of the egg (see Alvariño, Volume IVB of this series). Deficiency of regenerative power seen in chaetognaths is shared by animals with RNA-rich ova, a characteristic associated with absence of asexual reproduction (Ghirardelli, 1959b, 1965). Different animals of analogous evolution (e.g. Rotifera, Cladocera, Copepoda, Chaetognatha, Anura Amphibia) do not have the totipotent, or at least pluripotent cells which constitute the so-called embryonic reserve (Ghirardelli, 1968). Based on these observations, Ghirardelli (1958) stated that the regenerative ability of chaetognaths could not be as marked and effective as claimed by Kulmatycki (1918) and Pierce (1951).

Ghirardelli (1968) performed experiments on *Sagitta enflata* and *Spadella cephaloptera* from Villefranche-sur-Mer and the north Adriatic Sea, by cutting the animals at various levels of the body. Regeneration of the caudal fin is always rapid (from two to four days) if the posterior part of the body is not damaged. Epithelial cells in mitosis migrate towards the wound, and reconstruct the fin rays (Ghirardelli, 1959a). The lateral fins may be regenerated in seven to 10 days. The caudal region, if sectioned at a level *anterior* to the seminal vesicles, does not regenerate. The sectioned muscles fold in a scar made of alveolar stratified epidermis, reminiscent of an epithelial collarette. In some cases, the lateral fins fold towards the wound and fuse with the midline of the body, and there is no formation of seminal vesicles in the wounded caudal coelom, although normal development of the sperm proceeded. In such animals the sperm, however, cannot be extruded due to want of seminal vesicles. Therefore, no new cycle of male gametes would be possible as implied by Kulmatycki (1918) and Pierce (1951). On the contrary, if the cut passes through immediately *behind* the seminal vesicles, only a rudimentary regeneration of the caudal fin occurs.

Ghirardelli (1958) obtained regeneration of the caudal fin of *Spadella cephaloptera* beheaded immediately after amputation of the posterior end of the body, 56 per cent fin regeneration in decapitated animals against 36 per cent in those not decapitated. This may suggest that the presence of the head inhibits the regenerative process of the caudal fin, and that regeneration is only possible via the ventral ganglion.

Regeneration of the head does not occur, according to Ghirardelli (1956, 1959a), in *Spadella cephaloptera* and *Sagitta* (probably *S. bipunctata*). However, Pierce (1951) and other authors have observed specimens of *Sagitta setosa, S. minima, S. enflata*, and *S. euneritica* with heads that are abnormally small, and bearing no teeth or hooks. It is not clear from their accounts if that condition was produced by regeneration or what they saw was only a wounded head. Species of *Sagitta* may be beheaded by predators and, if the amputation occurred at the level of the ventral ganglion or in front of it, a sharp stump could be formed with histological features of a scar. This would indicate a lack of differentiation and of the regeneration process. Duration of the regeneration process and the chances of survival of the wounded animal are not known. The stumpy head is more rounded and the eyes can be seen, and there is doubt whether it is a case of true regeneration or only one of repair of a lesion on the cephalic region.

Pierce (1951) indicated that *Sagitta helenae* and *S. enflata* found with their heads cut off, together with a short section of the trunk, were at various stages of head regeneration. This condition was first attributed to accidental damage encountered in the net, but analyses of plankton samples have shown many specimens at various degrees of head regeneration. No regrowth of the posterior part of the body and tail was found. After the loss of the head, the trunk tissues contracted tightly together at the wounded end, giving the appearance of a sausage. The head began to form inside the contracted end, the eyes appearing first, followed by the mouth and the hooks (Alvariño, 1965).

Pierce (1941) stated that although he had examined hundreds of *Sagitta setosa* and *S. elegans* from the northern latitudes, no evidence of head regeneration was observed in these species.

Ghirardelli (1959c) reported young chaetognaths, probably *Sagitta bipunctata* and *S. enflata*, showing the beginnings of regeneration of the head. I have observed regeneration of the head in *S. elegans, S. enflata, S. euneritica, S. pacifica, S. neglecta*, and *S. pulchra* (Alvariño, unpublished).

III. PARTHENOGENESIS

This form of reproduction has not been investigated in chaetognaths. However, laboratory experiments with isolated individuals (Reeve, 1966), in which no copulation would occur, have shown that bursting seminal vesicles ejected sperm to the water, some of which would enter the receptaculum seminis. Only a few extruded ova were fertilized and those produced larvae, while the unfertilized ova invariably degenerated. It could therefore be assumed that parthenogenesis proper does not occur in Chaetognatha.

IV. FECUNDITY

The fecundity of *Sagitta elegans* has been calculated (McLaren, 1963, 1966) by setting ovary length against body length, and in turn relating the number of ova to ovary length. It appears that egg production by *S. elegans* is the function of adult size. The brood size is the result of the number of eggs produced by a functional female population. Egg number is equivalent to the number of ova carried by the parent, and it is a function of the size of the animal and the capacity of the ovary filled with ova. Comparisons must be made between animals of the same size, if a calibration were to be set up between parent size and egg number. The standardized number of eggs may then be used to compare the reproduction potential of a given species under different environmental conditions, within a restricted locality or over various areas in the wide distributional region of the species.

Breeding may be restricted to one or several seasons, or a succession of broods may be produced, as in *Sagitta enflata*. Therefore, simply put, the rate at which eggs are produced will be termed ‘fecundity’. The number of eggs produced per standard animal per species per unit of time (season) could be determined. Different species reach various adult sizes, in each of which the number of eggs is a function of the size of the animal. Fecundity can thus be defined as 'the number of eggs produced per individual per species and geographic location'.

Determination of the number of ova is easy in chaetognaths, the animals being transparent. The number of ova can be plotted against standard body weight or body length. Variability within species, time of year, and locality and over the years can so be observed. Differences are likely an expression of long-term cyclical fluctuations in reproduction level from year to year, related basically to food supply. Such differences and annual variations in egg production may be of importance in competition and dominance of chaetognath populations. The number of ova produced by chaetognaths is usually higher in 'poor' areas and in species living under stress (e.g. bathypelagic and cold-water species). Small numbers of ova — flat, elongated, and scattered along the ovaries — are observed in tropical populations carried out of their normal environmental living areas because of either scarcity of food or infestation with parasites (e.g. *Sagitta bierii* off Central American Pacific, *S. bedfordii* in some Indonesian locations). This confirms that food supply is a basic factor in the success of reproduction in chaetognaths as in many other animals. The number of ova in epipelagic populations is related to the size of the population: in large populations, the number of ova produced could be lower than in small populations.

To compare relative reproductive efficiency, there is a need to take into account the metabolic process, the number and size of eggs produced, and the time required for the production and hatching of eggs. Certain species can withstand severe climatic conditions advantageously by a marked seasonal breeding period, and by production of a relatively small number of large eggs. However, the same annual cycle could be maintained with a relatively large number of small eggs, leading to greater fecundity, and consequently greater competitive power. Large eggs produce larvae which are almost as large and as advanced in development as the juveniles — strong, able to feed, and better suited to survive.

V. STERILITY

Sterility, or poor reproductive ability, of *Sagitta scrippsae* off California (Alvariño, 1983) appears to be related to lack of adequate food to provide for the development of the gonads. *Sagitta bierii* inhabits the eastern Pacific from the United States to Chile, but populations off Central America do not seem to reproduce there due to high temperature and/or lack of the right kind of food in the area; the animals are all small with few flat ova (Alvariño 1964b, 1965, 1967). This observation leads us to suggest that *S. bierii* of Central American Pacific are likely descendants of specimens inhabiting the north and south of the region, mainly from the California- and Peru-Currents domain of the species (Alvariño, 1965, 1967). How higher temperatures can inhibit breeding is illustrated by *S. hispida*, a species unable to breed in the Biscayne Bay during the high water temperature of the summer.

Parasitism is another cause of arrest in gonadal development of chaetognaths, at least in some areas of the world: e.g. Gulf of Siam (*Sagitta bruuni, S. bedoti, S. pulchra*), the Caribbean (*S. enflata*), the Mediterranean (*S. enflata*), and off California mainly in the neighbourhood of Los Angeles (Alvariño, unpublished; and *S. scrippsae*:Alvariño, 1983). A high percentage of Chaetognatha here are infested with parasites (trematodes, cercarias), a strong indication of man-made pollution.

VI. REPRODUCTIVE CYCLES AND STRATEGIES

In *Sagitta friderici*, there is only one reproductive cycle, at the end of which the animals die (Cavalieri, 1963). Studies of abundance, distribution, and seasonal reproductive cycles of *S. elegans* indicate a life span of three months in Georges Bank (Clarke *et al.*, 1943); the animals die soon after breeding. In Georges Bank there is only one main breeding period per year. However, two populations of *S. elegans* may coexist there at least during part of the year, one indigenous to the area, and the other carried south from northern waters with the Labrador Current. Therefore, a wide size-range of maturity stages is encountered for *S. elegans* in the American North Atlantic. In the Georges Bank area, reproduction of *S. elegans* generally starts in April. Stage I animals present in September may represent the end of the spring and summer reproduction; those overwintering will produce a new generation next spring.

Two generations of *Sagitta elegans* were found in Bedford Basin by Zo (1973) with different life-history tactics: a spring generation which reached maturity in mid-September and reproduced during the rest of the year and an autumn generation (born from the spring generation) which apparently overwintered and reproduced during the next spring. Most of the young developed to maturity between June and September. This suggests that the successive hatching of eggs in spring provides a continuous recruitment of adults. The autumn generation, i.e. animals hatched during the autumn-winter period, grow slowly and reach maturity in the spring with increase in temperature and food availability. The larvae measure 1.28–1.30 mm. Autumn adults developed at 3.8°C have a mean length of 19.7 mm, while spring adults developed at a mean water temperature of 2.3°C are more than 25 mm long.

Sagitta enflata, which is abundant in temperate and tropical oceanic waters and has also invaded neritic regions, is probably the only epipelagic chaetognath to resort to the tactics of multiple cycles of maturity during its life span. As a result of this, the fecundity reaches a high level and the population becomes large and agglomerated in space leading to severe competition for food among the individuals. *Sagitta enflata* is also the chaetognath presenting the highest degree of cannibalistic behaviour, a possible regulator of population size.

Uninterrupted reproduction takes place in tropical and subtropical chaetognath populations; the rate of survival of the fall generation, however, is higher than that of the winter generation. Breeding index in the tropics is not constantly maintained through the year, and variations in density of the populations result from biotic and abiotic changes in the environment. Neritic species inhabit a region of drastic environmental fluctuations along the year, and consequently they show greater variation in density of population than oceanic species distributed over wide ranges. *Sagitta euneritica*, off California, exhibits great seasonal variation through the year (Alvariño, 1967). In species studied over a wide latitudinal range of their distribution, such as *S. bipunctata* and *Pterosagitta draco*, reproduction occurs throughout the year in the tropics, but only in spring and summer at temperate locations. This means that the reproductive span shortens coincidentally with the termic variations, which also affect changes in the food supply.

Annual breeding seasons are common to both Arctic and Antarctic regions. A large proportion of polar species brood their embryos and larvae (e.g. *Eukrohnia*) and release them as juveniles, when food is available. In species inhabiting deep waters, maturity takes place once a year as in polar species, but their life span may include, at least occasionally, several maturity cycles.

A. Reproductive and Developmental Delays

One mode of ensuring optimum reproductive and developmental success for a species is by temporally scheduling these processes to take place when conditions for survival of the progeny are favourable. Coming to strategic delays in reproduction and development, in *Eukrohnia*, 'diapause' in development of eggs and larvae may be regulated to favour hatching process at the right time for survival of the species as we have just seen above. Overwintering population of *Sagitta crassa* delay reproduction until food is plentiful for the larvae. Russel (1936) suggested that normal delay in development of gonads of late summer broods of many planktonic animals, including chaetognaths, is frequently accompanied by a descent of that population to deep strata, provoked by the removal of some essential factor "from the water during the summer, which becomes available again after a period of time or is perhaps lacking in the diminishing food supply". The significance of carotenoids, vitamins, and related substances in the plankton has only been tentatively investigated, but it is known that the carotenoid, vitamin and sterol constant varies greatly, not only in relation to the plankton but also to the season. Carotenoids and vitamin A within the plankton (Gillam *et al.*, 1939) begin to rise just about or at the spring diatom peak, the maximum being during the autumn. The peak coincides with the main breeding period of the plankton (Lucas, 1947).

It is well known that water-borne metabolites may influence reproduction. The conditioning of the environment through external products may bring about community integration through adaptation of animals to the products of others. The production of certain compounds may be related with reproduction of planktonic animals and induce particular stages of their life history. Local concentration of such compounds might tend to stimulate the development of maturing animals and the fertilization of eggs (Alvariño, 1989). Carnivores do not eat plants, but some of the substances available in plants are obtained by them through their prey. It would be of interest to develop research on the biological factors responsible for the variation and constitution of plankton communities and their influence in reproduction, spawning and breeding, hatching, and survival.

Water masses may have similar parameters of salinity and temperature but, in keeping with different plankton populations they harbour, differences in rate of reproduction between chaetognath species are not uncommon. These variations may depend on vital metabolites and other substances released to, or removed from, the waters. This is best illustrated by *Sagitta elegans* and *S. setosa*, dominant in plankton off England. Abundance of *S. elegans* is accompanied by plankton assemblages different from those of *S. setosa*; also, successful fish-larvae populations are related to dominance of *S. elegans* in plankton of the region. Appropriate combination of experiments suggests the presence of a 'beneficial' substance in both Celtic and Biscay Bay waters, and its lack in the local waters characterized by an abundance of *S. setosa*. The English Channel waters are characterized usually by *S. setosa* community, and the Celtic Sea and Bay of Biscay by *S. elegans* and other different planktonic communities. It appears that the Celtic and Biscay waters supply some necessary ingredients for successful reproduction, resulting also in an abundant fish population (Wilson and Armstrong, 1952). Alvariño (1989) showed that certain plankton assemblages ensure high reproductive success and high survival of anchovy larvae.

B. Breeding and Spawning Strategies

Reproductive success can be guaranteed only if suitable strategies are evolved by the species to synchronize breeding and spawning activities of its members and thereby to increase the chances of fertilization and production of the young. The simplest method of estimating reproductive activity of any species is the observation of breeding of animals in the field or in the laboratory. Such observations are imprecise but they produce important data on the presence of mature gametes, sperm, and ova. Spawning is not easy to induce when gonads are not gravid, but when the animal is gravid almost any stimulus may cause spawning, and also egg laying.

There is need to determine the factors inducing spawning in nature. It may be argued (see Giese and Pearse, 1973 for discussion) that in nature no spawning stimuli *per se* are required, and that spawning and breeding are spontaneous after the gonads have become mature. This hypothesis is, however, disputed as changes in biotic and abiotic factors and hormonal milieu are definitely known to play a role in inducing spawning in animals (see Volumes I and II of this series). *Sagitta tasmanica* specimens reaching the Gulf of Maine area grow larger than normal with large ovaries and well-developed full seminal vesicles, but there is no evidence of breeding perhaps because there the spawning stimulus is wanting. The animals may die and disappear either with no breeding or with a young population that does not survive. In any case, no *S. tasmanica* eggs have been reported from that area.

It is well known that light induces spawning and breeding (Knight-Jones, 1951; Kume and Dan, 1968; Segal, 1971) in animals. Exudates from green algae (Myazaki, 1938), diatom blooms (Barnes, 1957), and chemical exudates from males and females of the same species have been shown to synchronize breeding. Probably some of the most mature individuals, the best receptors of stimuli, are first induced to breed in nature and produce exogenous stimulants to other individuals in the population, until the synchronization phenomenon reaches epidemic proportions ensuring maximum fertilization.

Studies on bathymetric distribution of chaetognath species indicate that young and small specimens inhabit the upper oceanic layers, while full-mature and large individuals extend into deep waters. In other words, there is an ontogenic vertical distribution of the population down the water mass (Alvariño, 1964a, 1965). Our analysis of the bathymetric distribution of *Sagitta scrippsae* (open-closing net collections), off California, included specimens 10 to 50 mm long. Small-sized individuals appeared in the upper 225 m, and the largest in strata below. Young, Stage I individuals of *S. gazellae* inhabit the upper 250 m (Alvariño *et al.*, 1983) whereas Stage II appears mainly at 500 m to 1,000 m depth (David, 1955). Distribution of *S. elegans* in Bedford Basin (Zo, 1973) also showed an ontogenic bathymetric pattern of the populations. Observations on the ontogenic stratification of the chaetognath populations (Alvariño, 1964a) indicate that fecundation and laying of eggs take place in deep layers, and eggs and young are brought up to upper layers. Studies by Reeve and Cosper (1975) on *S. hispida* populations in the shallow waters of Biscayne Bay, Florida, indicate that surface waters rarely contain mature animals. In the eastern Canadian region, young *S. elegans* and *Eukrohnia* appear in the upper layers, while large individuals are at deep strata (Huntsman, 1919).

REFERENCES

Alvariño, A. (1964a). 'Bathymetric distribution of Chaetognaths', *Pac. Sci.*, **18**(1), 64–82; *Contrib. Scripps Inst. Oceanogr.*, **34**(1616), 39–57.

Alvariño, A. (1964b). 'Zoogeography of Chaetognatha, specially in the California Region. (Zoogeografía de los Quetognatos, especialmente de la region de California)', *Ciencia*, **23**(2), 51–74, *Contrib. Scripps Inst. Oceanogr.*, **34**(1705), 1677–1702.

Alvariño, A (1965). 'Chaetognaths', *Oceanogr. mar. Biol. Ann. Rev.*, **3**, 115–194.

Alvariño, A. (1967). 'Zoogeography of California: Chaetognatha (Zoogeografía de California: Quetognatos)', *Rev. Soc. Mex. Hist. Nat.*, **27**, 199–243, *Contrib. Scripps Inst. Oceanogr.*, **37**(2139), 487–531.

Alvariño, A. (1983). 'The depth distribution, relative abundance and structure of the population of the Chaetognatha *Sagitta scrippsae* Alvariño 1962, in the California Current off California and Baja California', *Anales del Instituto de Ciencias del Mar y Limnologia, Universidad Nacional Autonoma de Mexico (UNAM)*, **10**(1), 47–84.

Alvariño, A., Hosmer, S.C., and Ford, R.F. (1983). 'Antarctic Chaetognatha: United States Antarctic Research Program ELTANIN Cruises 8–28, Part I. American Geophysical Union. Biology of the Antarctic Seas XI', *Antarctic Research Series*, **34**, 129–338.

Alvariño, A. (1989). 'Abundance of zooplankton species, females and males, eggs and larvae of holoplanktonic species. Zooplankton assemblages and changes in the zooplankton communities related to *Engraulis mordax* spawning and survival of the larvae', *Mem. III Encontro Brasileiro de Plancton*, pp. 63–149.

Barnes, H. (1957). 'Processes of restoration of synchronization in marine ecology: The spring diatom increases and the "spawning" of the common barnacle, *Balanus balanoides* (L)', *Ann. Biol.*, **33**, 67–85.

Cavalieri, F. (1963). 'Nota preliminar sobre *Sagitta* (Chaetognatha) del litoral Atlantico Argentino', *Physis*, **24**(67), 223–236.

Clarke, G.L., Pierce, E.L., and Bumpus, D.F. (1943). 'The distribution and reproduction of *Sagitta elegans* on Georges Bank in relation to the hydrographical conditions', *Biol. Bull.*, **85**, 201–226.

David, P.M. (1955). 'The distribution of *Sagitta gasellae* Ritter-Zahony', *Discovery Rept.*, **27**, 235–278.

Ghirardelli, E. (1956). 'La rigenerazione in *Spadella cephaloptera* Busch', *Boll. Zool.*, **18**(2), 597–608.

Ghirardelli, E. (1958). 'La rigenerazione in *Spadella cephaloptera* Busch: Influenza del capo sulla rigenerazione della regione caudale', *Riv. Biol.*, **50**(2), 169–177.

Ghirardelli, E. (1959a). 'La struttura della pinne e la istogenesi rigenerativa in *Spadella cephaloptera* Busch.', *Pubbl. Staz. zool. Napoli*, **31**(1), 1–14.

Ghirardelli, E. (1959b). 'Osservazioni sulla deficienza dei poteri rigenerativi nei Chaetognati. Considerazioni sui rapporti fra riproduzione agamica e determinazione del ceppogerminale', *Atti Accad. Sci. Ist. Bologna*, Rc. 11, **6**, 1–15.

Ghirardelli, E. (1959c). 'Habitat e biologia della riproduzione nei Chetognati', *Arch. Oceanogr. Limnol.*, **11**(3), 1–18.

Ghirardelli, E. (1965). 'Differentiation of the germ cells and regeneration of the gonads in Planarias', in *Regeneration in Animals and Related Problems* (Eds. V. Kiortsis and H.A.L. Trampusch), pp. 177–184.

Ghirardelli, E. (1968). 'Some aspects of the biology of the chaetognaths', *Adv. Mar. Biol.*, **6**, 271–375.

Giese, A.C., and Pearse, J.S. (1973) (Eds). *Reproduction in Marine Invertebrates*, Vol. 1, Academic Press, New York, pp. 1–48.

Gillam, A.E., El Ridi, M.S., and Wimpenny, R.S. (1939). 'The seasonal variation in biological composition of certain plankton samples from the North Sea in relation to their content of vitamin A, carotenoids, chlorophyll and total fatty matter', *J. Exp. Biol.*, **16**, 71–88.

Huntsman, A.G. (1919). 'Some quantitative and qualitative plankton studies of the Eastern Canadian plankton. 3. A special study of the Canadian Chaetognatha, their distribution, etc. in the waters of the eastern coast', *Can. Fish. Exped. 1914–1915, Ottawa*, pp. 421–485.

Knight-Jones, E.W. (1951). 'Gregariousness and some other aspects of settling behaviour in *Spirorbis*, *J. mar. biol. Ass. U.K.*, **30**, 201–222.

Kulmatycki, W.J. (1918). 'Bericht uber die Regenerations-fahigkeit der *Spadella cephaloptera*', *Zool. Anz.*, **49**, 281–284.

Kume, M., and Dan, K. (1968). 'Introduction', in *Invertebrate Embryology*, Nobit Publ. House, Belgrade. pp. 1–7.

Lucas, C.E. (1947). 'The ecological effects of external metabolites', *Biol. Rev.*, **22**(3), 270–295.

McLaren, Ian A. (1963). 'Effects of temperature on growth of zooplankton and the adaptive value of vertical migration', *J. Fish. Res. Bd. Canada*, **20**(3), 685–727.

McLaren, Ian A. (1966). 'Adaptive significance of large size and long life of the chaetognath *Sagitta elegans* in the Arctic', *Ecology*, **47**, 852–855.

Myazaki, J. (1938). 'On the substance which is contained in green algae and induces spawning action of the male oyster (preliminary note)', *Bull. Japan. Soc. Sci. Fish.*, **7**, 137–138.

Pierce, E.L. (1941). 'The occurrence and breeding of *Sagitta elegans* Verrill and *Sagitta setosa* J. Muller in parts of the Irish Sea', *J. mar. biol. Ass. U.K.*, **25**, 113–124.

Pierce, E.L. (1951). 'The Chaetognatha of the West Coast of Florida', *Biol. Bull.*, **100**(3), 206–228.

Reeve, M.R. (1966). 'Observations on the biology of a chaetognath', in *Some Contemporary Studies in Marine Science* (Ed. H. Barnes), George Allen and Unwin, London, pp. 613–630.

Reeve, M.R., and Cosper, T.C. (1975). 'Chaetognatha', in *Reproduction of Marine Invertebrates*, Vol. II, *Entoprocts and lesser Coelomates* (Eds. A.C. Giese and J.S. Pearse), Academic Press, New York, pp. 157–181.

Russell, F.S. (1936). 'A review of some aspects of plankton research', *Rapp. Proc. Verb. Cons. Perm. Intern. Explor. Mer.*, **95**, 5–30.

Segal, E. (1971). 'Light, animals, invertebrates', *Mar. Ecol.*, **1**(1), 159–211.

Wilson, D.P., and Armstrong, F.A.J. (1952). 'Further experiments on biological differences between natural sea waters', *J. mar. biol. Ass. U.K.*, **311**, 335–349.

Zo, Z. (1973). 'Breeding and growth of the chaetognath *Sagitta elegans* in Bedford Basin', *Limnol. Oceanogr.*, **18**, 750–756.

Polyspecific Nature of Tuna Schools: Shark, Dolphin, and Seabird Associates

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Abstract.– Yellowfin tuna *Thunnus albacares* are commonly found associated with other species, especially sharks, birds, and dolphins, in the eastern tropical Pacific. Data from the purse seine fishery there, collected during 1974 and 1975, indicate that sharks occurred with tuna in 40% or more of the purse seine sets made around floating logs. Most other species, including rays, billfish, and small tunas, usually occurred in less than 10% of the sets. The association rate of these bycatch species declined progressively from log- to school- to porpoise-associated sets. This, together with their behavior as understood, suggests that at least some of these species stay with the tuna as much as they can. Such behavior would be like that of polyspecific associations in which two or more species travel together for foraging and protective advantages.

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Fishery Bulletin, U.S. 89:343–354 (1991).

Tuna are often found associated with other species, a behavior that is also seen among other schooling, herding, or flocking animals. While it is often convenient to think of any of these species as being effectively monospecific (single species) in behavior, there is growing awareness that polyspecific, enduring assemblages are common among higher animals. Such associations, comprised of several species that feed, interact, and travel together for periods of time, are not merely aggregations of animals along routes or points of common attraction. The specific interactions involved are not well understood, even though field observations have been intensive in some cases.

Mixed-species schools of fishes are frequently observed and caught. While usually seen as chance associations (e.g., Itzkowitz 1977), some species in these schools may obtain enhanced protective and foraging benefits (Ehrlich and Ehrlich 1972, Barlow 1974, Wolf 1987). Many such schools may therefore be polyspecific, and represent purposeful interactions.

Polyspecific bird flocks are common (Moynihan 1962; Morse 1970, 1977; Munn and Terborgh 1979). In some cases, over a dozen species move together through different environments with the composition of individuals and species apparently changing little (Hutto 1987). Diamond (1981) pointed out that polyspecific flocks often consist of similar core species that stay together, perhaps for years, maintaining flock characteristics and holding group territories. There are leader species, which are usually conspicuous, and follower species (Caldwell 1981, Greig-Smith 1978).

Mammals, with even more complex behaviors, abound with examples of polyspecific associations. Such associations have been noted in bats, cetaceans, often in ungulates, and particularly in the behaviorally versatile primates. Among the latter, species pairs of certain cercopithecid monkeys may be together 50% of the time, and it often appears that one species initiates and terminates the association, and uses the other to better discover food and detect danger (Struhsaker 1981, Cords 1987). Locally, these polyspecific associations are species-specific; other sympatric monkeys are apparently ignored and always by themselves (Gautier-Hion et al. 1983). This suggests that benefactor species are actively searched for by follower species. These associations, which vary in species composition by area, may last for days or months. Group territories may be defended. Similar behaviors have been observed in cebid monkeys, some of whose polyspecific associations appear to be permanent (Terborgh 1983). Interestingly, monkey species that appear to initiate and benefit from the polyspecific associations can be observed sometimes in front, sometimes at the rear, of traveling groups.

In general, polyspecific associations seem to form when social species of similar foraging ecology join to form larger groups to increase feeding success and to better avoid predators. The former may be ascribed to facilitation of feeding or to greater access to resource information (Clark and Mangel 1984). An additional benefit might be a lessening of intragroup competition (relative to monospecific groups of the same size). The enhanced safety could result from more effective vigilance (Pulliam 1973) or to the "convoy" effect (Olson 1964). It seems that the behaviorally more versatile species often exploit other species' behaviors, although there appear to be mutual benefits as well. For the most part, these polyspecific associations seem loosely coupled; the overt interspecies behaviors are circumstantial rather than obligatory, and generally agonistic. Species appear to join and leave the groups mainly in response to foraging situations; accordingly, they may be together for hours or days, sometimes months or even years.

In this paper I describe species found with tuna in the eastern tropical Pacific (ETP) and propose that tuna schools have a polyspecific nature. What this implies about tuna biology, especially that of the yellowfin *Thunnus albacares*, is discussed.

Data and methods

I used data collected by Southwest Fisheries Science Center (SWFSC) observers placed aboard U.S. tuna purse seiners. Such data have been available since 1966, but the records have not always been consistent or extensive with respect to other species caught with tuna (except for dolphins). The reasons include the pressure of observers' duties and the proprietary nature of fishing operations. After 1975, some kinds of bycatch information were no longer collected at all, and only abbreviated codes for certain other associated species were recorded.

The earlier, pre-1976 observer records, however, contain many candid notes on bycatches and other tuna associates, although even then the logs required only generic, not comprehensive, descriptions. Fortunately, some observers clearly were interested in tuna-associated fauna, and they frequently recorded detailed descriptions of what they saw.

I therefore selected records from the more information-rich 1974–75 database on purse seine sets (a "set" is a launch and retrieval of a purse seine net) for information on species that occur with tuna. I compiled a list of 22 observers personally known by myself or other SWFSC workers to have been reliable or to have had keen interest in pelagic fauna, and obtained pertinent information from their original logsheets. These logsheets constituted the set records of each of their 33 fishing trips. The trips occurred during all months except December, with 90% of the data collected between January and mid-June.

I examined the data pooled over all fishing trips and also by individual trip, since the quality of the records varied among observers. The data from one T.M. Duffy (TMD) is presented separately in the analysis below (TMD sets cf. the regular fleet sets) to illustrate how the actual observations of a particular observer could differ from the overall, pooled results. Duffy recorded information copiously and was an experienced and interested observer.

The data were divided into two areas and according to how the tuna were caught. The areas, delimited by latitudes 15°S and 25°N, were from the Central American coasts westward to 100°W ("off Central America") and from 100°W out to 135°W ("off Mexico") (see Figure 1). The first area contained sets mainly off the Central American coasts and southwestward to the Galapagos Islands; this is an important area for fishing both free-swimming and log-associated tuna, and also dolphin-associated tuna (explained below). The second area had sets mainly between southern Mexico and Clipperton Island, where much dolphin-associated tuna is taken. The tuna sets were further partitioned according to whether they were made around floating logs ("log–fish" sets), on free-swimming tuna ("school–fish" sets), or on dolphin-associated tuna ("porpoise–fish" sets). These are the terms used by the fishermen for the variously caught tuna, i.e., for different set types. The porpoise–fish sets refer to tuna caught usually with spotted and spinner dolphins, *Stenella attenuata* and *S. longirostris* (called "porpoise"). Table 1 gives the numerical breakdown of the 1762 purse seine sets I examined according to the above categories.

The purse seine sets in each area and set-type category were examined for frequency of different associated species to obtain a profile of the multispecies composition of the tuna schools. For each of certain species—actually grouped species because identifications were inexact—this frequency was expressed as the fraction (p) of the pertinent sets in which the species was caught. For comparison, I calculated both overall fractions considering all sets from all trips and arithmetic means of the fractions for individual trips. The latter fractions were computed only where fishing trips had more than ten sets in the category of interest. Binomial 95% confidence limits of the overall fractions were determined in accordance with the number of sets involved (n). Ranges were determined for the trip fractions. These latter fractions were statistically heterogeneous among trips, at least for log–fish and porpoise–fish sets. Thus the overall fractions probably best reflect the polyspecific composition of schools.

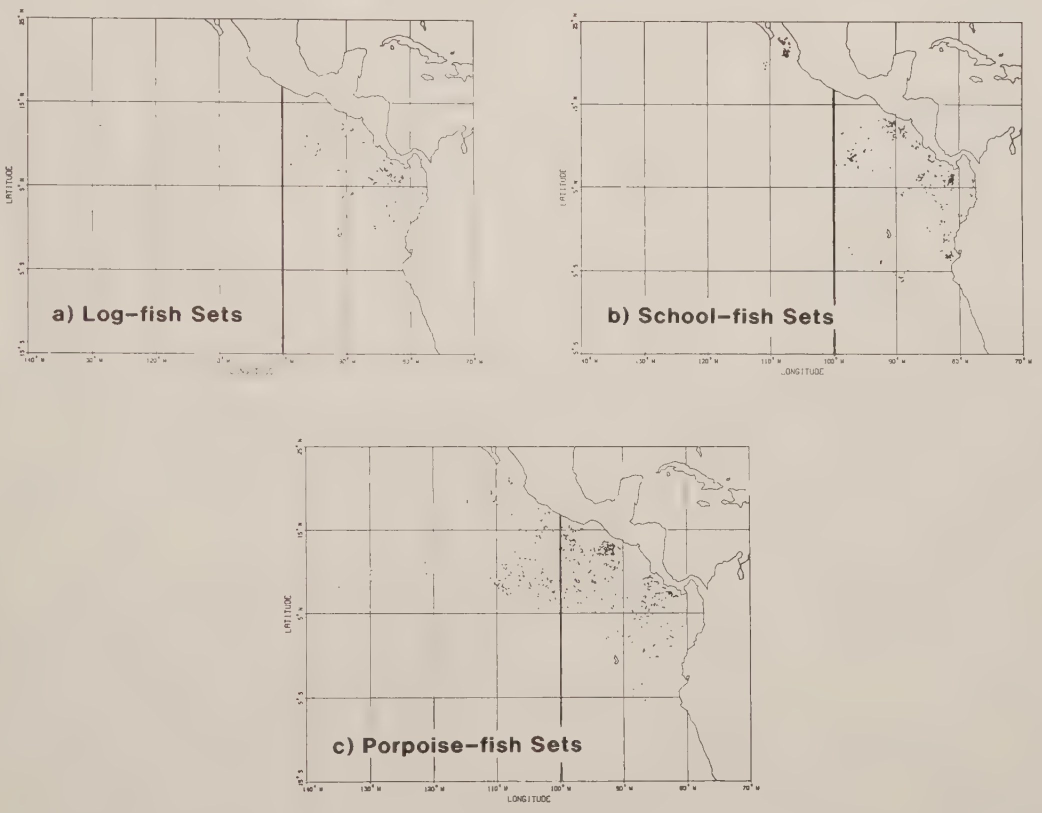

Figure 1

Locations of (a) log–fish sets, (b) school–fish sets, and (c) porpoise–fish sets inspected. Data were examined separately to the east ("off Central America") and west ("off Mexico") of longitude 100°W.

Related data gleaned from the records were summarized. These included information on size, abundance, and actual species composition within the species groups.

The species composition of bird flocks occurring with the tuna was described after ordering the (n) reported species in each flock according to (1 to n) decreasing ranks of abundance (again, the species were actually grouped species). This was done to circumvent differences in the accuracy with which different observers estimated species' flock sizes. The fraction of total flocks in which a bird species ranked at least 2 (i.e., was at least second most-abundant) was regarded as that species' importance value. When that value was 50% or more of the flocks in a category, that species was considered dominant for that set-type category. Several species could be "dominant" according to this criterion.

Both yellowfin, and skipjack *Katsuwonus pelamis*, tuna are sought by purse seiners, although yellowfin is usually preferred. Overall, yellowfin was captured in 78% of the log–fish sets, 57% of school–fish sets, and 99% of porpoise–fish sets examined (including sets capturing both tunas). The mean tonnages of yellowfin caught per set, based on "successful sets," are given in Table 1. Successful sets are those catching more than 1 ton of yellowfin and/or skipjack tuna.

Tunas from the different set types are likely to behave differently, since younger yellowfin tend to associate with floating logs in nearshore waters while older, larger fish tend to be with dolphins farther offshore (Greenblatt 1979). Therefore, the species associations

Table 1

Characteristics of yellowfin tuna sets examined for other-species associations according to log-fish, school-fish, and porpoise-fish set types.

		Off Central America			Off Mexico		
		Log	School	Porpoise	Log	School	Porpoise
Fleet data	Total sets	185	438	540	2	104	220
	SS Ratio[1]	0.69	0.61	0.80	—	0.54	0.92
	YF tons[2]	6.5	6.8	8.9	—	5.7	8.2
	(n)	102	145	379	—	51	192
	2 SE[3]	1.3	1.2	1.1	—	1.5	1.2
TMD[4] data	Total sets	58	65	78	1	1	70
	SS Ratio	0.74	0.57	0.85	—	—	0.83
	YF tons	6.0	7.5	11.8	—	—	7.4
	(n)	34	22	49	—	—	60
	2 SE	1.4	1.7	1.3	—	—	1.3

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[1] The Successful Set (SS) Ratio = fraction of total sets catching more than 1 ton of yellowfin and/or skipjack tuna. On porpoise-fish sets, the SS Ratio pertains to sets on *Stenella* dolphins only.

[2] Geometric mean short tons of yellowfin tuna (YF) per set, based on successful sets only; n is the size of the sample. Not all successful sets caught yellowfin.

[3] The multiplication-division factor for mean YF tons/set giving its 95% confidence interval.

[4] Observer T.M. Duffy (fleet data exclude these data).

with tuna, as seen in this study, will be discussed in terms of the ontogeny of yellowfin behavior.

Results

The fractions (p) of purse seine sets measuring the association rates of different (grouped) species are given in Table 2 (off Central America) and Table 3 (off Mexico). These fractions (expressed as percentages) are for the fleet sets, and they are summarized graphically in Figure 2. Figure 3 shows the association fractions for the T.M. Duffy (TMD) sets. In the tables, those species whose association rates differed significantly (χ^2, $P<0.05$) among set types are indicated by asterisks. For these, one can determine which of the set types was actually different by noting which of the mean rates occurred outside the 95% confidence intervals for the other set types.

Sharks clearly stood out among the fishes found associated with tuna. Overall, 40% of log-fish tuna sets took sharks. There was a progressive decline in this percentage to 10%, from log- to school- to porpoise-fish sets. Off Mexico, however, porpoise-fish sets may have been more likely to catch sharks (lower graphs in Figures 2 and 3). How commonly sharks may associate with tuna is emphasized by the TMD data (Fig. 3); individual fishing trips, of which this data from a single observer are an example, can experience shark occurrence rates of up to 90% on log-fish sets. The silky shark *Carcharhinus falciformis* was the most commonly reported species (25.2%) (Table 4). These sharks averaged 29.2 individuals in sets that caught them. However the range was large, from 1 to 500 per set. Other carcharhinids recorded were each under 10% of the identified sharks. Of these, the whitetip shark, frequently recorded with porpoise-fish sets (especially off Mexico), was most likely the oceanic whitetip *C. longimanus*, (R. Rasmussen, SWFSC, pers. commun.). Other less-common sharks included the whale shark *Rhincodon typus*. This species can be locally common off Baja California, where it is often associated with skipjack tuna. Sizes of the sharks caught with yellowfin were seldom recorded; however, it is known that medium- to large-sized specimens that are considered dangerous are often caught. The few sizes recorded ranged from 1.7 to 2.1 m. Many were simply described as "large." Others, described as "small" or comprising "25 tons" of catch, were probably all small-sized.

Rays occurred mainly in school-fish and porpoise-fish sets, the former more often. The records indicate that most were medium- to large-sized manta rays (Mobulidae). They occurred in groups of 1 to 2 on average, though up to 12 were recorded in some sets (Table 4).

Billfish (Istiophoridae) co-occurred with tuna in about 9% of the sets overall and more often off Central America than off Mexico. The association rates were similar among all set types, except for the TMD data

Table 2

Fraction (p) of purse seine sets (n) having various associated "species," off Central America (coast to 100°W).

		Fleet sets[1]						
		Overall fraction			Mean of trip fractions			
Associated spp.	Set type[2]	p (%)	n	95% CI[3]	p (%)	n/T	Range (%)[3]	Comments
Birds	L	83*	185	76–89	79	144/8	36–100	Birds very common with schools. Virtually all porpoise–fish sets are with birds.
	S	80	438	75–84	82	404/13	43–100	
	P	98	540	96–99	98	497/17	89–100	
Sharks	L	40*		32–48	37		21–77	Sharks common to very common with log–fish sets, but decreasingly so from log– to school– to porpoise–fish sets.
	S	21	″	17–26	20	″	0–61	
	P	13		10–17	13		0–36	
Rays	L	1*		0–3	1		0–7	Rays more often with school–fish sets than with porpoise–fish; rather seldom with log–fish.
	S	10	″	7–13	10	″	2–18	
	P	5		3–8	4		0–18	
Billfish	L	8		5–13	7		0–25	Billfish sometimes more frequent with log–fish sets, otherwise, similarly frequent among all school types.
	S	9	″	6–12	11	″	3–35	
	P	9		6–12	7		0–23	
Bullet tuna	L	10*		6–16	8		0–23	Bullet tuna often with logs; decreasingly so with school– and porpoise–fish sets.
	S	4	″	2–6	4	″	0–17	
	P	1		0–3	<0.5		0–5	
Black skipjack	L	12*		7–18	15		0–40	Black skipjack more often with log–fish sets; not with porpoise–fish.
	S	5	″	3–8	5	″	0–19	
	P	0		0–1	<0.5		0–2	
Turtle	L	3*		1–7	4		0–9	Turtles infrequent and without trend among the different tuna set types.
	S	5	″	3–8	4	″	0–13	
	P	1		0–3	1		0–6	
Dolphinfish	L	24*		18–31	27		0–50	Dolphinfish mainly with log–fish sets.
	S	7	″	5–10	7	″	0–26	
	P	2		1–4	3		0–23	
Yellowfin and skipjack tuna	L	66*	127	57–74	62	78/5	27–82	Skipjack common with school– and especially log–fish sets; seldom with porpoise–fish.
	S	40	266	34–46	45	225/10	8–63	
	P	3	392	1–6	2	325/12	0–8	

[1] Fleet sets are the data without T.M. Duffy sets; see text.

[2] Set types are log–fish (L), school–fish (S), and porpoise–fish (P) types.

[3] 95% CI of p's are from the binomial distribution. Trip fractions (n/T) are n sets from only those T trips having ≥ 10 sets. Asterisks indicate statistical significance among set types ($P \leq 0.05$).

which showed billfish significantly more frequent in log–fish sets (Fig. 3). Those rates ranged from 20% to 43% on different fishing trips. Sailfish *Istiophorus platypterus* comprised 31.4% of the billfish, the remainder being marlin. Several of the latter were identified as striped marlin *Tetrapturus audax* and black

Table 3

Fraction (p) of purse seine sets (n) having various associated "species," off Mexico (100–135°W).

		Fleet sets[1]						
		Overall fraction			Mean of trip fractions			
Associated spp.	Set type[2]	p (%)	n	95% CI[3]	p (%)	n/T	Range (%)[3]	Comments
Birds	L	—*	—	—	—	—	—	Birds very common with schools; virtually all porpoise-fish sets are with birds.
	S	77	104	68–85	72	80/4	50–100	
	P	98	220	93–100	98	169/6	91–100	
Sharks	L	—*		—	—		—	Sharks may be less frequent with school- than with porpoise-fish sets; cf. Table 2.
	S	6	″	2–12	3	″	0–11	
	P	13		7–21	14		0–43	
Rays	L	—		—	—		—	Rays similarly frequent with school- and porpoise-fish sets.
	S	9	″	4–16	8	″	0–18	
	P	5		2–11	5		0–8	
Billfish	L	—		—	—		—	Billfish relatively infrequent with both school- and porpoise-fish sets.
	S	4	″	1–10	5	″	0–9	
	P	3		1–8	5		0–23	
Bullet tuna	L	—		—	—		—	Rare in all set types.
	S	1	″	0–5	1	″	0–3	
	P	0		0–4	0		0–0	
Black skipjack	L	—		—	—		—	Not recorded.
	S	0	″	0–4	0	″	0–0	
	P	0		0–4	0		0–0	
Turtle	L	—		—	—		—	Relatively rare in all sets.
	S	3	″	0–8	1	″	0–3	
	P	3		0–8	4		0–9	
Dolphinfish	L	—*		—	—		—	Dolphinfish more often with school- than porpoise-fish sets.
	S	14	″	8–22	14	″	0–32	
	P	1		0–5	2		0–8	
Yellowfin and skipjack tuna	L	—*		—	—		—	Skipjack more often with school- than porpoise-fish sets; cf. Table 2.
	S	36	56	27–45	22	33/2	0–43	
	P	12	202	6–20	14	153/5	0–39	

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[1] Fleet sets are the data without T.M. Duffy sets; see text.

[2] Set types are log-fish (L), school-fish (S), and porpoise-fish (P) types.

[3] 95% CI's are from the binomial distribution. Trip fractions (n/T) are n sets from only those T trips having ≥10 sets. Asterisks indicate statistical significance among set types ($P \leq 0.05$).

marlin *Makaira indica* (Table 4). The blue marlin *M. nigricans* was not present on the records examined, but occurs in the area. Usually 1 or 2 marlin were captured. Records of measured or estimated sizes show that some fish were large, e.g., a 3.2m sailfish and a 4.4m (total length) marlin. A swordfish *Xiphius gladius* was also recorded in one of the sampled sets.

"Bullet" tuna (*Auxis* sp.) and black skipjack *Euthynnus lineatus* are small tunas often taken in large numbers—but usually recorded in tons—in log-fish sets off Central America. Bullet tuna and black skipjack were very seldom in porpoise-fish sets. The association rate for bullet tuna was 10% for fleet log-fish sets and 41% for TMD log-fish sets (Table 2; Figs. 2, 3).

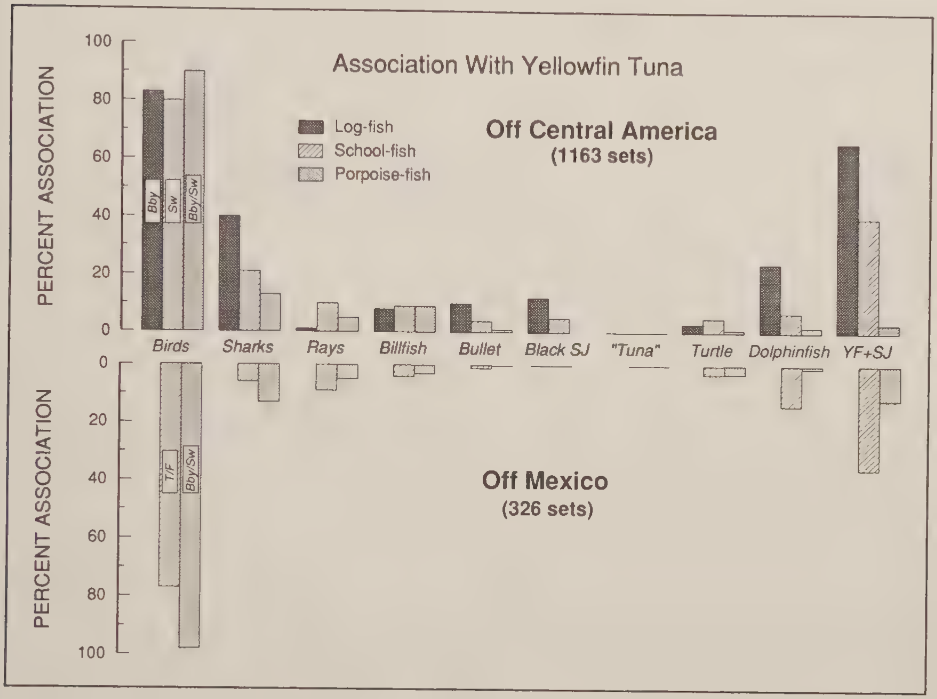

Figure 2

Percent association of different "species" with yellowfin tuna in fleet samples. Bby = boobies, Sw = shearwaters, T = terns, F = frigatebirds, "Tuna" = unspecified tuna species, YF = yellowfin tuna, SJ = skipjack tuna.

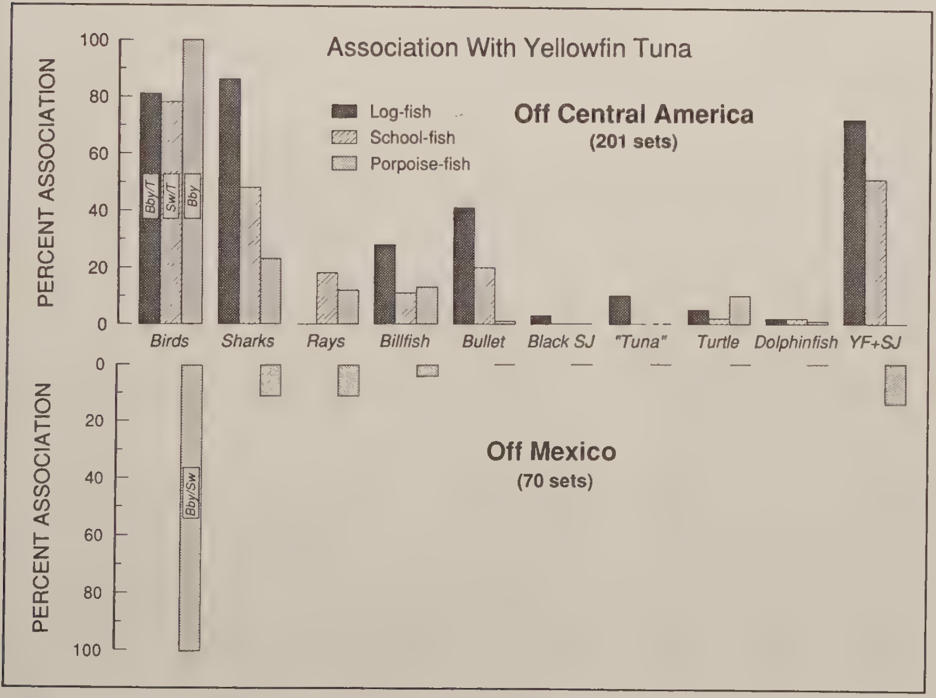

Figure 3

Percent association of different "species" with yellowfin tuna in T.M. Duffy samples. Bby = boobies, T = terns, Sw = shearwaters, "Tuna" = unspecified tuna species, YF = yellowfin tuna, SJ = skipjack tuna.

Table 4
Characteristics of tuna-associated species.

Species	Species[1] percent	Numbers of individuals/set[2] Mean	Numbers of individuals/set[2] Range
Shark or "carcharhinid"	49.1	23.4	1–350
Silky (*Carcharhinus falciformis*)	25.2	29.2	1–500
Whitetip (*C. longimanus*)	9.0	5.1	1–39
Other carcharhinids (bull, "requiem," "brown," blacktip, gray)	6.1	11.6	1–80
Hammerhead (*Sphyrna* spp.)	3.9	2.3	1–7
Thresher (*Alopias* spp.)	3.2	3.6	1–28
Mackerel/Mako/White (Lamnidae)	2.4	8.3	1–40
Blue (*Prionace glauca*)	0.5	1.0	—
Whale (*Rhincodon typus*)	0.5	1.0	—
All (*N*409)	(100.0)		
Ray	15.0	1.1	1–2
Manta (Mobulidae)	75.0	1.6	1–12
Others (Sting, bat, skate)	10.0	1.1	1–2
All (*N*118)	(100.0)		
Swordfish (*Xiphias gladius*)	—	1.0	—
All (*N*1)	(100.0)		
Billfish (Istiophoridae)			
Marlin (*Tetrapturus audax, Makaira indica*)	68.6	1.3	1–5
Sailfish (*Istiophorus platypterus*)	31.4	1.4	1–6
All (*N*159)	(100.0)		
"Turtle" or Ridley (*Lepidochelys olivacea*)	87.5	1.4	1–4
Others (leatherneck, green)	12.5	2.5	1–3
All (*N*24)	(100.0)		
Dolphinfish[3] (*Coryphaena hippurus*)	63.2	6.0	1–200
Amberjack/yellowtail (*Seriola* spp.)	30.5	11.8	1–100
Pompano (*Trachinotus*?, Kyphosidae?)	6.2	22.5	1–100
All (*N*144)	(100.0)		
Wahoo (*Acanthocybium solandri*)	76.2	2.9	1–25
Spanish mackerel/mackerel (*Scomberomorus, Trachurus*?)	23.8	17.8	1–50
All (*N*42)	(100.0)		
Ocean sunfish (*Mola mola*)	—	1.7	2–3
All (*N*3)	(100.0)		

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[1] From all data. Refers to species composition among individuals that could be identified or categorized.
[2] In sets that caught the species.
[3] Not including dolphinfish reported with other species absent.

Turtles were relatively infrequent in the tuna purse seine sets, at rates generally less than 5% overall and without evident pattern among the three set types. Most (21 of 24) were recorded as "turtle" or identified as Ridley turtles *Lepidochelys olivacea*, as probably most were (pers. observ.) (Table 4). A few leatherback turtles *Dermochelys coriacea* and green turtles *Chelonia mydas* were also identified.

Dolphinfish (*Coryphaena* spp.) were most frequent (24%) in log-fish sets and progressively rarer in school-fish and porpoise-fish sets. Individual fishing trips had log-fish sets with association rates ranging from zero to 50%. Considering that dolphinfish are frequently associated with flotsam and are not strong

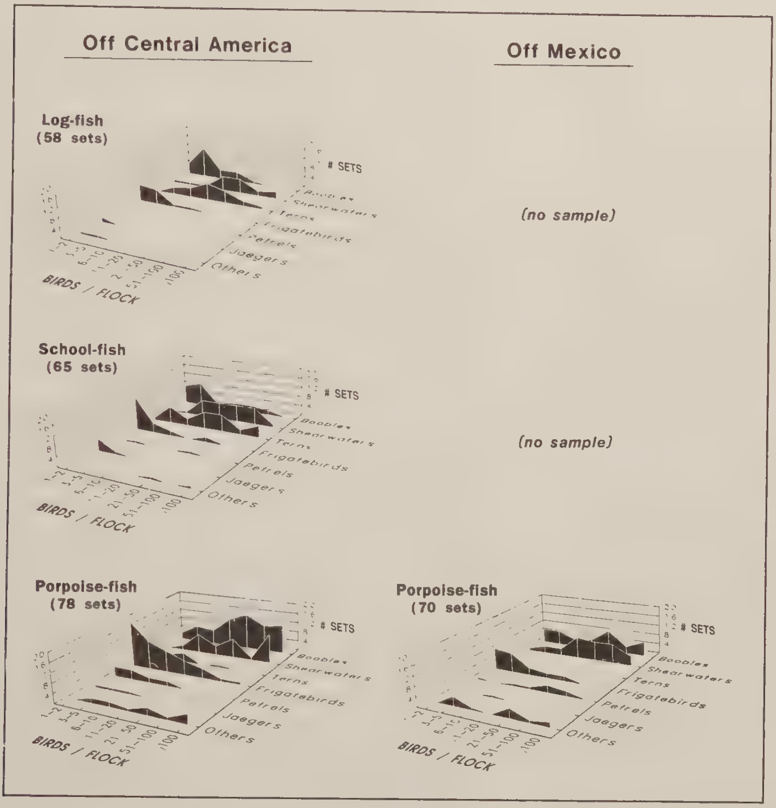

Figure 4

Histogram envelopes of bird flock sizes off Central America and off Mexico according to log–fish, school–fish, and porpoise–fish set types. Each histogram plots frequency (# SETS) against the species' abundance in the flocks (BIRDS/FLOCK). T.M. Duffy samples only.

swimmers like tuna, those trips with low occurrence rates may represent separation of this species from tuna during capture. When captured together with tuna, and with other associated fishes as well, dolphinfish averaged 6 individuals per set, with the range from 1 to 200 (Table 4).

Several other miscellaneous fishes were caught rather persistently, especially in log–fish sets. Notable among these were yellowtail or amberjack (*Seriola* sp.) and wahoo *Acanthocybium solandri* (Table 4). Others, such as triggerfish (Balistidae) were common and were probably associated with the flotsam near which the tuna were caught; these small fish are frequently seen under such objects (pers. observ.).

The fraction of successful (not total) purse seine sets that took both yellowfin and skipjack tuna measures the likelihood of these two tunas being associated. Yellowfin and skipjack were together in nearly 70% of successful log–fish sets. This fraction declined markedly in school-fish sets and even more so in the porpoise-fish sets, i.e., to 3% or less (Table 2).

The largest category of other animals associated with tuna was seabirds (Figs. 2, 3). Birds have a close relationship to tuna (and tuna fishing to birds), and observers usually record some aspect of their presence. Approximately 80% of log–fish and school–fish sets were in company with birds, and birds were present with virtually all porpoise–fish sets, regardless of area. The dominant bird species, as identified by the importance-ranking criterion, were usually boobies (*Sula* spp.) or boobies and shearwaters (*Puffinus* spp.) with log– and porpoise–fish sets; in the school–fish sets, the dominants were shearwaters or shearwaters and terns, *Sterna* especially (labeled histograms in Figures 2 and 3). The distribution of flock sizes of component species from the single-observer TMD data (Fig. 4) shows an increase in flocks and flock sizes of frigatebirds (*Fregata* spp.) and especially boobies in porpoise–fish sets relative to the other set types. Also, large tern flocks occurred primarily with school–fish sets. There was a shift toward larger shearwater flocks in the porpoise–fish sets off Mexico; the identifications indicate these were wedge-tailed shearwaters *Puffinus pacificus*.

Discussion

As yellowfin tuna grow, they become involved in changing species associations, some of which are polyspecific in nature, i.e., like the associations studied elsewhere that seem situation-dependent, opportunistic, and often casual. This is reflected in the changing pattern in the association rates (p) from log–fish to school–fish to porpoise–fish sets on tuna; it is this pattern, rather than the actual rate values, that is of significance. The rates themselves should be used cautiously as they are derived from data affected by observer interest and from samples that were not large.

Foraging associates

Logs, or other floating objects, seem to provide opportune sites for development of species associations. Not only can logs attract prey and predators, but they can also drift to convergences where species gather. The behavior of predators feeding near flotsam is not simple, however. If the arrival rate of prey should decrease sufficiently, a passively feeding predator may switch to active, wide-ranging foraging (see Gerritsen 1984).

The very common association of sharks with tuna and the strong decrease in this association from log– to school– to porpoise–fish sets suggest that sharks mostly encounter tuna near flotsam. Then, like gray reef sharks (carcharhinidae) that follow feeding carangid fish for leftovers (Enewetak Is., pers. observ.), these sharks might follow the yellowfin as both scavengers and predators. Such behavior is probably of decreasing advantage as the tuna grow and forage more widely and at faster speeds. The tuna themselves, in some situations, may be attracted to sharks, as they are to whale sharks (Stretta and Slepoukha 1986).

The overall association rate for most other species with yellowfin tuna averaged in the 10% range, including that of billfish, rays, turtles, and smaller tunas. The marlins probably follow tuna both as parasitic foragers and as predators; they share many prey species with tunas and also eat tunas, especially the smaller specimens (see Shomura and Williams 1975). Unlike the sharks, however, these powerful fish appear to have little difficulty keeping up with fast-moving tuna; their association rates did not appear different among set types. Manta rays and turtles probably represent the opposite situation, where the tuna initiate and maintain the associations, perhaps as an extension of their proclivity to investigate flotsam. This may be why rays tended to be taken more often in the school–fish sets. The large schools of black skipjack, bullet, and skipjack tunas that are frequently taken with log-associated yellowfin may be obtaining feeding and protective advantages, but these benefits likely decrease as the yellowfin grow. The smallest tunas would find it increasingly difficult to swim at the speed of the yellowfin, and the danger of predation by the larger fish would also increase. It is first the black and bullet tunas that decrease in school–fish sets; finally even skipjack become scarce in the sets on the large, porpoise-associated yellowfin.

The most conspicuous and strong association with tuna is that of seabirds. Most bird species can feed independently of tuna, but they feed closely with these fish at every opportunity. The flocks of terns and smaller shearwaters that feed with free-swimming tuna of school–fish sets suggest that these fish of mainly nearshore waters feed on abundant, smaller prey. The larger, more mature tuna are farther offshore, feeding on sparser but evidently still-rich food patches. Dolphins and the larger seabirds, i.e., boobies and wedge-tailed shearwaters, feed with them (see also Au and Pitman 1986). The dominating importance of boobies in both porpoise–fish and log–fish sets suggests they forage by a wide and fast-ranging search for all discontinuities at the sea surface, including that of surface-schooling tuna and dolphins. Such foraging would be particularly effective offshore, for the yellowfin there have been found to prey more on fish (i.e., on larger but likely more patchily distributed prey) and less on crustaceans than do nearshore-caught yellowfin (Olson and Boggs 1986).

The porpoise–fish sets are themselves a category of species association, although not treated above as such. The highly mobile dolphins and the tuna of these sets appear to feed actively together; they share many of the same prey species (Perrin et al. 1973).

Enhanced foraging may be the main advantage of polyspecific associations involving the larger, more mobile species of tropical, pelagic seas; this may stem from converging foraging tactics among these animals. Just as boobies and shearwaters race about over a feeding tuna school to maximize interceptions of fleeting and unpredictably surfacing prey, yellowfin and other large species, on a larger scale, should range rapidly over large expanses to find sparse and unpredictable, yet relatively rich, prey patches. Food overlap would be increased by such nomadic foraging (see Huey and Pianka 1981), and strong patchiness of prey should itself reduce the tendency of each species to exploit different spatial intervals of the spectrum of prey distribution (see Terborgh and Stern 1987).

Polyspecific tuna and dolphins

The tuna–dolphin association of the ETP is the association most similar to the polyspecific associations studied among primates and terrestrial birds, in that specific species appear to forage together without strong or obvious interactions. However, virtually all porpoise–fish sets are attended by birds that appear to be closely following the feeding tuna (Au and Pitman 1986). That and the high 80–90% successful set ratio of these sets compared with the other set types (Table 1) suggest that dolphins do not commonly feed with birds that are not also with tuna. These specific dolphins that feed with tuna are ecologically successful (i.e., abundant, especially relative to other non-tuna-associated dolphin species; Au and Pitman 1988). And since these dolphins are largely found within the habitat of surface-schooling yellowfin in the ETP (see Allen 1985 for distributions), and not the converse, it could be that dolphins exploit the feeding behavior of tuna more often than the reverse. If so, this would agree with what seems typical in polyspecific associations, that it is the behaviorally more-adaptive species that takes advantage. Considering further the opportunistic, casual nature typical of polyspecific associations, one should not be surprised that tuna and dolphins are not intimately associated in many other seas and even in certain areas within the ETP. Moreover, if either the tuna or the dolphins were to be overexploited where they are associated, dire (or propitious) consequences to the other of the pair need not be expected.

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Citations

Allen, R.L.
1985 Dolphins and the purse-seine fishery for yellowfin tuna. *In* Beddington, J.R., R.J.H. Beverton, and D.M. Lavigne (eds.), Marine mammals and fisheries, p. 236–252. Allen and Unwin, Inc., Winchester, MD.

Au, D.W.K., and R.L. Pitman
1986 Seabird interactions with dolphins and tuna in the eastern tropical Pacific. Condor 88(3):304–317.
1988 Seabird relationships with tropical tunas and dolphins. *In* Burger, J. (ed.), Seabirds and other marine vertebrates, p. 174–212. Columbia Univ. Press, NY.

Barlow, G.W.
1974 Extraspecific imposition of social grouping among surgeonfishes (Pisces: Acanthuridae). J. Zool. (Lond.) 174: 333–340.

Caldwell, G.S.
1981 Attraction to tropical mixed-species heron flocks: Proximate mechanisms and consequences. Behav. Ecol. Sociobiol. 8:99–103.

Clark, C.W., and M. Mangel
1984 Foraging and flocking strategies: Information in an uncertain environment. Am. Nat. 123(5):626–641.

Cords, M.
1987 Mixed-species associations of *Cercopithecus* monkeys in the Kakamega Forest, Kenya. Univ. Calif. Press, Berkeley, Los Angeles, and London.

Diamond, J.M.
1981 Mixed-species foraging groups. Nature (Lond.) 292: 408–409.

Ehrlich, P.R., and A.H. Ehrlich
1972 Coevolution: Heterotypic schooling in Carribean reef fishes. Am. Nat. 107(953):157–160.

Gautier-Hion, A., R. Quris, and J.P. Gautier
1983 Monospecific vs. polyspecific life: A comparative study of foraging and anti-predator tactics in a community of *Cercopithecus* monkeys. Behav. Ecol. Sociobiol. 12:325–335.

Gerritsen, J.
1984 Size efficiency reconsidered: A general foraging model for free-swimming aquatic animals. Am. Nat. 123(4):450–467.

Greenblatt, P.R.
1979 Associations of tuna with flotsam in the eastern tropical Pacific. Fish. Bull., U.S. 77:147–155.

Grieg-Smith, P.W.
1978 The formation, structure and function of mixed-species insectivorous bird flocks in west African savanna woodland. Ibis 120:284–295.

Huey, R.B., and E.R. Pianka
1981 Ecological consequences of foraging mode. Ecology 62(4):991–999.

Hutto, R.L.
1987 A description of mixed-species insectivorous bird flocks in western Mexico. Condor 89:282–292.

Itzkowitz, M.
1977 Social dynamics of mixed-species groups of Jamaican reef fishes. Behav. Ecol. Sociobiol. 2:361–384.

Morse, D.H.
1970 Ecological aspects of some mixed-species foraging flocks of birds. Ecol. Monogr. 40:119–168.
1977 Feeding behavior and predator avoidance in heterospecific groups. Bioscience 27:332–339.

Moynihan, M.
1962 The organization and probable evolution of some mixed species flocks of neotropical birds. Smithson. Misc. Collect. 143:1–140.

Munn, C.A, and J.W. Terborgh
1979 Multi-species territoriality in neotropical foraging flocks. Condor 81:338–347.

Olson, F.C.W.
1964 The survival value of fish schooling. J. Cons. 29:115–116.

Olson, R.J., and C.H. Boggs
1986 Apex predation by yellowfin tuna (*Thunnus albacares*): Independent estimates from gastric evacuation and stomach contents, bioenergetics, and cesium concentrations. Can. J. Fish. Aquat. Sci. 43:1760–1775.

Perrin, W.F., R.R. Warner, C.H. Fiscus, and D.B. Holts
1973 Stomach contents of porpoise, *Stenella* spp., and yellowfin tuna, *Thunnus albacares*, in mixed species aggregations. Fish. Bull., U.S. 71:1077–1092.

Pulliam, R.H.
1973 On the advantages of flocking. J. Theor. Biol. 38: 419–422.

Shomura, R.S., and F. Williams (editors)
1975 Proceedings, International Billfish Symposium, Kailua-Kona, Hawaii, 9–12 August 1972. Part 3, Species synopsis. NOAA Tech. Rep. NMFS SSRF-675, 159 p.

Stretta, J.M., and M. Slepoukha
1986 Analyse des facteurs biotiques et abiotiques associas aux bancs de thons. *In* Symons, P.E.K., P.M. Miyake, and G.T. Sakagawa (eds.), Proc. Int. Skipjack Year Prog. Symp., p. 161–169. ICCAT Spec. Publ., Madrid.

Struhsaker, T.T.
1981 Polyspecific associations among tropical rain-forest primates. Z. Tierpsychol. 57:268–304.

Terborgh, J.
1983 Five new world primates. Princeton Univ. Press, Princeton.

Terborgh, J., and M. Stern
1987 The surreptitious life of the saddle-backed tamarin. Am. Sci. 75(3):260–269.

Wolf, N.G.
1987 Schooling tendency and foraging benefit in the ocean surgeonfish. Behav. Ecol. Sociobiol. 21:59–63.

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THE SARDINE-ANCHOVY RECRUITMENT PROJECT (SARP): RATIONALE, DESIGN AND DEVELOPMENT

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ABSTRACT

The SARP species complex is a major factor in world fisheries production, a key trophic basis for other valuable stocks, and notoriously variable and prone to population collapse. SARP was selected as the initial focal project of the International Recruitment Project, which is part of the Ocean Science and Living Resources Program of IOC and FAO because of (1) the need to address within-year variability in survival and (2) the opportunity provided by newly developed technologies. The comparative method is a major element in the SARP project design. SARP projects have been implemented in European waters, in the Southwest Atlantic, in the upwelling region of the Southeast Pacific, off California and off Japan.

INTRODUCTION - OSLR

There is growing concern that various trends of global change (accumulation of atmospheric greenhouse gases and other anthropogenic effects such as pollution, overfishing, coastal development, etc.) may have major effects on marine ecosystems and the living resources that they contain. In any particular region, evidence of subtle trends tends to be submerged in large-amplitude natural interyear and inter-decadal local variability. However, greenhouse gases accumulate on a global scale and the other major anthropogenic trends are also occurring globally. It thus makes sense to look for effects globally. Part of the rationale behind the development of the IOC - FAO Program of Ocean Science in Relation to Living Resources (OSLR) is that by analyzing events in similarly functioning marine ecosystems distributed around the world, global patterns of events related to significant global trends must ultimately appear from within the "noise level" of naturally-occurring regional climatic variability. In fact, certain regional ecosystems (e.g., the Mediterranean, etc.) appear to be in advance of certain of the global trends and can provide early case histories. Once such patterns are identified, and credibly linked to progressive trends, they can constitute a basis for real prognostic capability with which to guide adaptive actions by governments, industries, and individuals. This rationale also supports the goal of developing enhanced marine scientific capabilities around the world with which to deal with the challenges ahead.

Variability in "recruitment" of younger fish into an exploited population has been recognized as the key unsolved problem hindering more effective management of living marine resources. Accordingly, an International Recruitment Program (IREP) was established as the initial subprogram of OSLR.

More recently a new OSLR subprogram on Harmful Algal Blooms has been established in response to the rapid global increase in economic and public health problems associated with toxic and anoxic algal-related phenomena. Many scientists believe that a worldwide epidemic of harmful species may be fostered by growing incidence of marine eutrophication and spread by human activities such as ships' ballast water discharges (Anon. 1990).

At the most recent meeting of the OSLR Guiding Group of Experts (February 1990) a third OSLR subprogram, Ecosystem Dynamics and Living Resources (EDLR), was proposed. This was in recognition of the evolution of OSLR activities toward system integration and to provide a natural interface with such programs as IGBP, GLOBEC, ECOMONOC (Russian), BICED (Brazilian), etc., and with other major IOC programs:

Ocean Dynamics and Climate, Marine Pollution, etc. The potential effects of Global Climate Change on living marine resources are intended to be a major focus of EDLR.

IREP

Lack of scientific understanding of the mechanisms controlling recruitment variability is widely recognized as the key problem area in fishery science at the present time (the term "recruitment" refers to the quantity of younger fish surviving the various egg, larval, and juvenile stages to begin to be captured in a fishery). Recruitment in most fish populations varies erratically from year to year in ways that cannot presently be explained or predicted. The unexplained large-amplitude variance obscures the essential underlying signals needed to manage and preserve the populations over longer time scales. These signals include the functional form of the relationship of expected recruitment to stock size, declines in stock productivity, effects of interspecies interactions, and reactions to habitat alterations, pollution, climate change, etc. Lacking the ability to resolve these signals, the methodologies of fishery science must rely on arbitrary assumptions and extreme simplifications concerning the very factors that control these outcomes. Collapses of important fishery stocks around the world continue to occur, with serious socioeconomic consequences. Moreover, as we now seem to be facing the prospect of unprecedented monotonic trends in ecosystem processes, associated with atmospheric greenhouse effects and other anthropogenic impacts, management schemes based on the old assumptions (quasi-random variation about some stable mean state, etc.) which have not worked well in the past can be expected to be even less effective in the future. Proclaiming the need for holistic management of our marine ecosystems is a very popular activity at the present time. However most would agree that a sound scientific basis on which to proceed is far from in place. Real improvement in the situation does not appear likely until significant advances in scientific understanding of mechanisms controlling recruitment variability can be realized.

The paradigm that has provided the framework for most of the previous advances in fishery science generally involves aggregation of information, temporally and spatially, into composite annual data points. The IREP rationale is to attempt to move beyond the restrictive conventional paradigm to address the richly detailed temporal and spatial patterns which exist within seasonal periods and both within and among regional habitats. A key goal is to develop coherent conceptual frameworks within which generic questions can be posed. Broad intra- and inter- regional application of the comparative method is seen as a means to develop the multiple differing realizations needed to draw scientific inference in a problem area where experimental controls are unavailable. Well-posed high resolution studies, both high temporal resolution "within year" exercises, along with complementary high spatial resolution studies, offer rational approaches to addressing key questions. Developmental activity within IREP has been oriented mainly toward two major projects: The Sardine - Anchovy Recruitment Project (SARP) and the Tropical Demersal Recruitment Project (TRODERP).

THE COMPARATIVE METHOD AND SARP

The experimental method and the comparative method have been called the two great methods of science (Mayr 1982). The experimental method is the method of choice when experiment al conditions can be readily controlled. The comparative method offers an alternative in cases where experimental controls may be impractical. As an example of its power, Mayr credits "nearly all the revolutionary advances in evolutionary biology" to the comparative method.

Bakun (1989) provides an overview of the problems involved in applying the experimental method to the recruitment problem. The ocean-atmosphere system is largely uncontrollable. Moreover, the mixture of scales of motion in the ocean makes it virtually impossible to maintain the integrity of the volume of water in which an experiment is taking place unless it is artificially contained in some manner. However, artificial containment restricts the scales of crucial dynamic processes and also presents anomalous interfaces and substrates which can alter essential mechanisms. Most importantly, because of the enormous reduction in numbers that occurs, survival of an individual to the age at which recruitment occurs is a very rare event compared to the fates of the overwhelming majority of hatchlings. The results obtained for most samples of larvae may be quite irrelevant to eventual recruitment at the population level. Thus experiments should ideally be performed at the population level. And if experiments on small population segments are difficult, the problems of performing experiments at the population level are overwhelming.

Although it is undeniably useful for certain issues (such as physiological requirements and responses of individuals, etc.) which may be validly be addressed in small controlled volumes, the experimental method has only limited utility with respect to the general problem of recruitment variability in marine populations. Thus the comparative method is the available, and logical, alternative. Accordingly, the comparative approach has become a key element in the design of SARP project activities.

THE SARP CONCEPTUAL DESIGN

The SARP "within-year" exercise

The SARP high temporal resolution "within-year" exercise, developed under the leadership of Ruben Lasker and his colleagues at Southwest Fisheries Center, has been identified as a uniquely promising process-oriented approach for addressing the mechanisms and impact of short term temporal variability in larval survival (Anon. 1983,1984,1987). The within-year exercise consists basically of three operational elements: (i) a determination of short-period (ideally two weeks or less) variation in the production of larvae within a spawning season, (ii) the establishment of a birthdate distribution of juveniles originating from that production, and (iii) an observational program to specify simultaneous variation in potential explanatory variables, which may include physical, chemical, and biological processes and properties. The ratio between the curves developed in elements "i" and "ii"constitutes a "survival index" which identifies periods (cohorts) with particularly good survival or particularly high mortality. A particular attribute of this approach is that it addresses the problem at the population level, rather than addressing the fate of typical or "average" larvae which, as discussed above, may be irrelevant to net reproductive success. It does this by relying on the capture of survivors, i.e., members of the successful subset, at a later life cycle stage and then reconstructing its birth date from daily marks carried in the bony structures (Pannela 1971, Methot 1983, Campana and Neilson 1985). Comparison of the survival index to short term variability in environmental processes and conditions developed in element "iii" may reveal linkages and causal mechanisms. Another key ingredient in the formulation of the SARP within-year exercise is application of newly-developed technological tools such as the larval birthdating methodology, histological measures of starvation (Theilacker 1986) and immunoassays of predator stomach contents (Theilacker et al. 1986).

Implicit in the concept is a loss of spatial resolution within the larval habitat because the animals may undergo substantial movements during the period between birth and capture. This may not be a crucial drawback because the most energetic sources of short-term environmental variability (atmospheric storms, etc.) have large spatial scales. Actually, any source of increased mortality that did have both a short temporal scale and a small spatial scale, could not have any substantial effect on net annual recruitment to fish populations whose spawning is distributed on a regional scale over an extended spawning season.

In order to produce a valid "survival index" from larval or juvenile birthdate frequencies it is necessary to adjust for short term variability in larval production. Since larval production can vary on small spatial scales as well as on small temporal scales, a full SARP "within-year" exercise requires detailed monitoring of larval production over the entire habitat at short intervals over an extended period. This is one of the most demanding aspects of the operation. Because of the extensive ship time and other operational resources required, no fully elaborated SARP "within year" exercise, incorporating a full suite of environmental and biological (histological, etc.) diagnostic procedures, has been completed to date.

Broadening the concept (high spatial resolution, etc.)

In view of this, participants in the Ad Hoc SARP Consultation (Anon. 1989b) have recommended that the SARP concept should be broadened to include other types of high-resolution (both temporal and spatial) studies. The original SARP "key phrases": high-resolution, new technologies, and inter-regional comparative studies would continue to characterize SARP activities.

Technologies for indicating short term variability in larval growth rates, both biochemically (Buckley 1984) and by measurement of otolith increment width (Gutierrez and Morales-Ninn 1986) are available. Starvation and predation appear to be the major sources of larval mortality (Hunter 1981). These are both associated with growth rate. Starvation represents the extreme of minimal (negative) growth rate. Vulnerability to predation appears to be size dependent (Hunter 1981) and so growth rate would affect predation mortality. A focus on factors controlling growth rate variation would provide a high temporal resolution verification field without the onerous necessity for the detailed specification of larval production (Bakun, 1989). Also, since the very recent growth may be determined, spatial resolution is restored. The availability of spatial resolution allows many new hypotheses to be addressed. These would include effects of topographically-controlled hydrodynamic structures and frontal formations, effects of eddies and current meanders, etc., and all the associated hypotheses concerning larval retention (Sinclair 1987), local enrichment, convergence, advection, etc.

Participants in the 1989 Ad Hoc SARP Consultation suggested adoption of some particular research "themes" for SARP that could be addressed at a variety of activity levels in various regional settings but could promote a steady accumulation of insight. Some possibilities are listed in the report of that meeting (Anon. 1989). The consensus of the Consultation was that the prototype SARP "Within-year" exercise should continue to be an important aspect of the SARP strategy, but the lack of resources to implement this particular exercise should not preclude valid and valuable participation in SARP.

PRESENT STATE OF ORGANIZATION AND IMPLEMENTATION OF SARP

The SARP project was created at the "Workshop of the IREP Component of the IOC Programme on Ocean Science in relation to Living Resources" in Halifax in 1983 following suggestions by Ruben Lasker (Anon. 1983). It was then initiated at a second workshop in La Jolla in 1984 where detailed proposals for SARP projects in South America and California where formulated. However, perhaps because the SARP rationale is multi-disciplinary and somewhat outside the "mainstream" of conventional fishery science, none of these proposals received funding, and the field work was delayed for several years. Only recently have SARP proposals attracted substantial funding support.

The European SARP (EUROSARP) is a cooperative project of five European laboratories: Lisboa University, Instituto Espanol de Oceanografia, Plymouth Marine Laboratory, Hamburg University, and the Alfred-Wegener Institute of Polar and Marine Science in Bremerhaven. It is receiving the core funding from the Directorate General for Fisheries of the Commission of the European Community. The project was initiated in 1990 and concentrates on North Sea sprat (Sprattus sprattus), the sardine (Sardina pilchardus) off northern Spain and the anchovy (Engraulis encrasicholus) in Portuguese estuaries. The project includes the "high temporal resolution" exercise as well as "high spatial resolution" studies.

The Southwest-Atlantic SARP was initiated in late 1989 by a cooperative multi-national cruise with the German research vessel "METEOR" funded by the German Research Association (DFG), the German Ministry for Research and Technology (BMFT), IOC, the bilateral programmes for marine research between Argentina, Brazil, and Germany, and authorities of the five participating countries. A multi-disciplinary team of biologists and physical oceanographers from Argentina, Brazil, Germany, Sweden, and Uruguay carried out the field work. The samples and data are processed in the laboratories of the five countries. Communication is facilitated by frequent exchanges of scientists between different laboratories. This project has concentrated so far on the high spatial resolution exercise on a single species, the Southwest Atlantic anchovy (Engraulis anchoita) the spawning area of which extends over 2800 km along the shores of southern Brazil, Uruguay , and northern Argentina comprising a whole suite of diverse environments. The rationale of this project is described in Anon. 1989a.

Implementation of operational SARP field activities in the. eastern South Pacific has made only slow progress due to funding difficulties. However, it is expected that the SARP initiatives for anchovies and sardines off Chile, Peru, and Ecuador as suggested in 1984 by the workshop in La Jolla will eventually be funded in view of the pressing problems of the fisheries and fish industry in this region and of the need for insight into effects of predicted global climate changes. In contrast to the status of the operational approach, the inferential approach, as elaborated in the report of the IREP Workshop in Halifax in 1984 (Anon. 1984), has been successfully implemented in a cooperative project on the "Peruvian Anchoveta and its Upwelling Ecosystem" supported by IMARPE/GTZ/ICLARM. This activity presented an example of an innovative way to study recruitment of the Peruvian anchoveta (Engraulis ringens) and other components of the Peru Current ecosystem and also provides a model for assembling and presenting regional data so as to support multilateral progress via the comparative approach. The results are published in two substantial volumes (Pauly and Tsukayama 1987 and Pauly et al.1989).

The Centro de Investigacion Cientifica y Educacion Superior de Ensenada (CICESE) in Baja California initiated a programme on the dynamics of recruitment of Pacific sardine (Sardinops sagax caerulea) in the Gulf of California. Of particular interest are the interactions with the anchovy (Engraulis mordax) population which has recently entered the Gulf. Associated with this research is a study on the historical abundance of sardines and anchovies in the Gulf using fish scales preserved in varves from laminated sediments.

The Japanese BIOCOSMOS (SARP) project on population dynamics of the Japanese sardine (Sardinops melanostica) was initiated in 1989 and funded for ten years. The ultimate goal of this multi-disciplinary project, in which a number of different laboratories is involved, is to forecast future population variations.

In addition, several Mediterranean countries are considering initiating SARP on their anchovy or sardine stocks. A scheme of the structure of the OSLR programme including the SARP initiatives is given in Fig. 1. The SARP programme since 1984 has been under the auspices of the Guiding Group of Experts for OSLR. Recently, to cope with the needs for coordinating an expanding SARP programme, particularly in view of the increased levels of activity in other OSLR elements due to the addition of the EDLR and HAB sub-programmes, a special Guiding Committee for SARP was established in 1990.

Over the last 18 months, activity in the regional SARP projects has increased considerably. SARP has clearly shifted from the phase of implementation into a second phase which is characterized by continuous sampling at sea, processing of samples, analysis of data in different regions of the world, and integration of the results generated by the various operational and inferential approaches.

EMERGING GENERALIZATIONS

The various studies completed within the SARP project and within associated scientific programmes appear to be converging toward a general pattern wherein a combination of three general factors is associated with favorable reproductive habitat for anchovies and sardines. These factors are:

1. Enrichment of the food web by physical processes (upwelling, mixing, etc.);

2. Opportunity for concentrated patch structure of food particles to accumulate (stability, lack of active turbulent mixing, and/or strong convergence in frontal structures);

3. Availability of mechanisms promoting retention of larvae within (or transport of larvae to) appropriate habitat.

The processes involved in these three factors are not generally mutually compatible. For example, upwelling is a response to divergent horizontal flow. Upwelling and convergence therefore cannot directly coincide. Likewise mixing may lead to enrichment but destroy vital small scale structure in food particle distributions. Coastal upwelling, being induced by offshore surface transport, is directly linked to loss of larvae from the coastal habitat. The wind that drives the upwelling also mixes the upper ocean layer, destroying its structural stability. Thus, the three factors can combine favorably only in special environmental configurations. Each factor must be present to a sufficient degree, but not to so overwhelming a degree as to preclude the others. Alternatively, the favorable configurations may involve temporal and spatial lags that allow effects of opposing processes to be mutually supportive

For example, applying the comparative method to seasonal and geographical aspects of habitat climatology Bakun and Parrish (1991) have diagnosed three separate configurations used by a single extended anchovy (Engraulis anchoita) population off the coasts of Argentina, Uruguay, and southeastern Brazil. The recent multinational SARP cruise in the Southwest Atlantic by the German vessel METEOR has tended to corroborate these findings (Anon. 1989a, Alheit et al. 1991). The most common favorable configuration for eastern ocean coastal regions (Parrish et al., 1983) appears to be that of a coastal bight downstream of an upwelling center (Fig. 2a). This is apparently the configuration used by the clupeoid fish populations, Engraulis anchoita and Sardinella brasiliensis, spawning within the Southeastern Brazilian Bight. However, southward along the coast of South America, conditions change and Engraulis anchoita uses two distinctly different environmental configurations to extend its reproductive habitat.

Off Uruguay and adjacent regions of Argentina and Brazil, Surface Ekman transport tends to be directed onshore, which is opposite to the direction that would induce coastal upwelling. However, the hydrographic situation of this wide, abruptly-breaking continental shelf generates substantial upwelling at the shelf break. The onshore Ekman transport would serve to carry the upwelling-based nutrients and enriched production onto the inner shelf habitat, where the continent itself serves as a shield from the large-scale westerly winds and relatively low wind- mixing rates result. Relatively strong water column stability is favored by confluence of different water masses associated with the various alongshore boundary flows, by strong seasonal surface heating in the wind sheltered region, and by substantial fresh water input. The areas of water mass confluence, including fronts associated with the freshwater outflows, represent convergence zones which may serve to concentrate distributions of larval food particles. Certainly the onshore-directed surface Ekman transport facilitates the retention of eggs and larvae within the shelf habitat. This second configuration (Fig. 2b) would seem to have a strong analog in the spawning grounds of the South African anchovy population (Parrish et al., 1983).

On the Patagonian Shelf off Argentina, strong tidal mixing over the inner continental shelf results in a third configuration (Fig. 2c). In some shallower locations the water column is homogenized from surface to bottom. The result is that surface water in the mixed areas is of greater density than the surface water of the adjacent stratified areas. Similarly, the bottom water is of lesser density than that of the stratified areas. Thus the less dense surface water of the stratified offshore zone tends to override the denser mixed water, leading to onshore flow in the surface layer toward a convergent surface front. The heavier bottom water of the stratified zone tends to wedge under the lighter mixed water, leading to onshore flow also in the bottom layer. To balance these gravity-driven onshore flows at the surface and bottom, the mixed waters find their equivalent density level within the stratified water column and move offshore in the mid-depth thermocline. The upward mixing of deeper waters in the mixed water column injects dissolved plant nutrients into the illuminated surface layers. Resulting phytoplankton growth may be further concentrated in the convergent frontal zones. Also the rather stable situation within the thermocline, shielded from surface mixing processes by the lighter waters above and from bottom generated turbulence by the heavier layer below, may favor patch formation, swarming, and other processes leading to concentration of small organisms in the trophically-enriched waters moving offshore from the mixed zone (Valenzuela et al. 1991). Retention of larvae near the frontal zone could be ensured by appropriate vertical migratory behavior to utilize the onshore flow in the surface or bottom layers. And on the larger scale, the general onshore wind-driven surface Ekman transport would serve to prevent major loss of larvae from the shelf habitat. Association of anchovy larvae with the frontal structures has been demonstrated on the recent SARP Cruise of the METEOR.

Cury and Roy and their collaborators have combined the comparative approach with - sophisticated time series analysis to further bolster the general pattern that is emerging. Roy et al. (1989) explain the gross seasonal and geographical aspects of the spawning strategies of African clupeoid stocks north of the Equator in terms of two limiting factors, planktonic production (related to enrichment processes) and environmental stability (which they associate with both larval retention and lack of turbulent mixing). In fact, Roy (1990) points out that the observed spawning habits of that group of stocks fall into a pattern wherein the spatial locations of spawning grounds appear to particularly optimize larval retention while the seasonal aspects of spawning appear to be tuned in a way that particularly limits exposure to turbulent mixing of the water column. Cury and Roy (1989) have analyzed recruitment time series for various clupeoid stocks of West Africa, Peru, and California; their time-series analysis, utilizing new nonlinear empirical techniques, indicates a consistent "optimal environmental window" (i.e., an intermediate band of wind speeds, neither so high as to cause undue turbulent mixing and offshore transport nor so low as to yield insufficient trophic enrichment via upwelling and mixing) wherein reproductive success is favored. Very recent extention of their analysis to additional stocks (California anchovy, Moroccan sardine) continue to consistently yield the dome-shaped "optimal environmental window" pattern (Roy et al. 1991).

Various univariate correlative relationships between recruitment and one or another of the three primary factors have been published over the years. In view of the new insights now being developed, it is not surprising that a specific environmental configuration and a specific biological life style could combine to make variability in a particular single factor stand out from the others in its correspondence to year class survival. But it is also not surprising that such relationships, which only reflect part of the causal "equation", often break down unexpectedly. For example, an increasing trend in wind speed, by increasing upwelling, might favor good recruitment up to a point where the concentration and the retention factors are unduly disrupted. Continued increases in wind may then become detrimental.

Increased upwelling and mixing are generally reflected in lower sea surface temperatures, as is increased offshore transport due to its linkage to upwelling. Increased stability, or onshore transport of oceanic surface waters in a coastal upwelling region, tends to be reflected in warmer sea surface temperature. Thus, temperature is often found to be correlated with year class success. However the recent results call attention to the fact that the relationship may not be direct but only a reflection of the interaction of dynamic processes. Certainly, a pelagic fish would generally be able to compensate for any direct detrimental effects of anomalous temperatures merely by adjusting its depth level. For example, the anchovy inhabits the surface layer off Patagonia, which is toward the poleward end of its range. However, in the Southeastern Brazilian Bight, which is toward the tropical end of its range, it is found within or beneath a shallow thermocline and at the surface only within cool plumes of recently upwelled water (Matsuura et al., 1985). Thus temperature alone appears to be an uncertain and somewhat precarious indicator of environmental effects on year class success.

We are finding that tropical outbreaks (e.g, El Nino) and other instances of anomalous dominance of tropical waters and conditions (e.g., lack of normal penetration of productive temperate water masses into the coastal habitat off Southeastern Brazil) appear to be generally detrimental to local reproductive success. However, rather than being attributable to direct effects of the associated warm temperatures, the detrimental effects are most often ascribed to suppression of the enrichment factor during these episodes. Other types of warm anomaly often appear to favor reproductive success of anchovies and sardines (Bakun, in press).

REFERENCES CITED

Alheit, J., J. de Ciechomski, C. Ebel, M. Ehrlich, J.-C. Elgue, L. Djurfeldt, G. Mantero, Y. Matsuura, H. Mianzan, W. Nellen, C. Odebrecht, F. Ramirez, R. Sanchez, G. Shaffer and M.D. Vinas 1991. SARP studies on Southwest Atlantic anchovy, Engraulis anchoita, off Argentina, Uruguay and Brazil. ICES C.M. 1991 / L:46

Anon. 1983. Workshop on the IREP Component of the IOC Programme on Ocean Science in Relation to Living Resources (OSLR). IOC Workshop Rep. 33. Intergovernmental Oceanographic Commission, Unesco, Paris. 51pp.

Anon. 1984. IOC-FAO Guiding Group of Experts on the Programme of Ocean Science in Relation to Living Resources, First Session. Reports of Meetings of Experts and Equivalent Bodies SC-84/WS/18. Intergovernmental Oceanographic Commission, Unesco, Paris. 34pp.

Anon. 1987. IOC-FAO Guiding Group of Experts on the Programme of Ocean Science in Relation to Living Resources, Second Session.Reports of Meetings of Experts and Equivalent Bodies SC-87/WS/41. Intergovernmental Oceanographic Commission, Unesco, Paris. 37pp.

Anon. 1989a. Second IOC Workshop on Sardine / Anchovy Recruitment Project (SARP) in the Southwest Atlantic. IOC Workshop Report No. 65. Intergovernmental Oceanographic Commission, Unesco, Montevideo, Uruguay 21-23.August 1989.

Anon. 1989b. IOC Workshop Report of the Expert Consultation on the Sardine/Anchovy Recruitment Programme (SARP). IOC Workshop Rep. 66. Intergovernmental Oceanographic Commission, Unesco, Paris.

Anon. 1990. IOC-FAO/OSLR Ad hoc Group of Experts on Harmful Algal Blooms, Paris, 31 January - 2 February 1990. IOC/INF-817. Intergovernmental Oceanographic Commission, Unesco, Paris. 23 pp. + 4 annexes.

Bakun, A. 1989. Recruitment in fishery resources and its relation to environment: Accessible pathways to greater insight. pp. 25-34. In: Memorias del Simposio International de los Recursos Vivos y las Pesquerias en el Pacifico Sudeste, Via del Mar, 9-13 mayo, 1988. Rev, Pacifico Sur (Numero Especial). Comision Permanente del Pacifico Sur (CPPS).

Bakun. A. In press. The California Current, Benguela Current, and Southwestern Atlantic Shelf ecosystems: a comparative approach to identifying factors regulating biomass yields. In: K. Sherman, L.M. Alexander and B. Gold (eds.) Stress Mitigation and Preservation of Large Marine Ecosystems. American Association for the Advancement of Science.

Bakun, A. and R.H. Parrish. 1990. Comparative studies of coastal pelagic fish reproductive habitats: the Brazilian sardine (Sardinella aurita). J. Cons. Explor. Mer. 46: 269-283.

Bakun, A. and R.H. Parrish. 1991. Comparative studies of coastal pelagic fish reproductive habitats: the anchovy (Engraulis anchoita) of the southwestern Atlantic. J. Cons. int. Explor. Mer. (In press, August 1991 issue).

Buckley, L.J. 1984. RNA-DNA ratio an index of larval fish growth in the sea. Mar. Biol. 80: 291-298.

Campana, S.E. and Neilson, J.D. 1985. Microstucture of fish otoliths. Can. J. Fish. Aquat. Sci. 42, 1014-1032.

Cury, P. and Roy, C. 1989. Optimal Environmental window and pelagic fish reproductive success in upwelling areas.Can. J. Fish. Aquat. Sci. 46, 670-680.

Gutierrez, E. and Morales-Nin, B. 1986. Time series of daily growth in Dicentrarchus labrax L. otoliths. J. Exp. Mar. Biol. Ecol. 103: 163-179.

Hunter, J.R.1981. Feeding ecology and predation of marine fish larvae, p. 33-79. In R. Lasker (ed.) Marine Fish Larvae. Wash. Sea Grant. Program, Univ. Washington Press, Seattle, London. 131 p.

Matsuura, Y., Amaral, J.C., Sato, G., and Tamassia, S.T.J. 1985. Ocorrencia de peixes pelagicos e a estrutura oceanografica da regiao entre o Cabo de Sao Tome (RJ) e Cananeia (SP), em Jan-Fev/1979. Ser. Doc. Tec., PDP/SUDEPE, Brasilia, no.33, p3-70.

Mayr, E. 1982. The Growth of Biological Thought. Harvard Univ. Press, Cambridge, Mass. 974pp.

Mendelssohn, R. and Mendo, J. 1987. Exploratory analysis of anchoveta recruitment off Peru and related environmental series, p. 294-306. In D. Pauly and I. Tsukayama (eds.) The Peruvian Anchoveta and Its Upwelling Ecosystem: three Decades of Change. ICLARM Studies and Reviews 15. Instituto del Mar del Peru (IMARPE), Callao, Peru; Deutsche Gesellschaft fur Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines. 351 pp.

Methot, R.D., Jr. Seasonal variation insurvival of larval northern anchovy (Engraulis mordax) estimated from the age distribution of juveniles. Fish. Bull., U.S. 81: 741-750.

Pannella, G. 1971. Fish otoliths: daily growth rings and periodical patterns. Science 173: 1124-1127.

Parrish, R.H., Bakun, A., Husby, D.M. and Nelson, C.S.1983. Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish reproduction. p.731-778. In: G.D. Sharp and J. Csirke (eds.) Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources. FAO Fish. Rep. 291. 1224pp.

Pauly, D. and Tsukayama, I., (eds.) 1987. The Peruvian Anchoveta and Its Upwelling Ecosystem: Three Decades of Change.ICLARM Studies and Reviews 15. Instituto del Mar del Peru (IMARPE), Callao, Peru; Deutsche Gesellschaft fur Technische Zusammenarbeit (GTZ) GmbH, Eschborn, Federal Republic of Germany; and International Centerfor Living Aquatic ResourcesManagement (ICLARM), Manila, Philippines. 351pp.

Pauly, D., Muck, P., Mendo, J., and Tsukayama, I., (eds.) 1989. The Peruvian Upwelling Ecosystem: Dynamics and Interactions. ICLARM Conference Proceedings 8. Instituto del Mar del Per (IMARPE), Callao, Peru; Deutsche Gesellschaft fr Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines. 438pp.

Roy, C. 1990. Reponses des stocks de poissons pelagiques a la dynamique des upwellings en Afrique de L'Ouest: analyse et modelisation. These de Doctorat. Universite de Bretagne Occidentale, Brest, France. 149 pp.

Roy, C., Cury, P., Fontana, A. and Belveze, H. 1989. Statgies spatio-emporelles de la reproduction des clupids des zones d'upwelling d'Afrique de l'Ouest. Aquat. Living Resour. 2: 21-29.

Roy, C., Cury, P. and Kifani, S. 1991. Optimal environmental window and pelagic fish reproductive strategy in upwelling areas. International Symposium on Benguela Trophic Functioning. Capetown, 8-13 September 1991. 26 pp. (in manuscript form).

Sinclair, M. 1987. Marine Populations. Univ. Washington Press, Seattle and London. 252 pp.

Theilhacker, G.H. 1986. Starvation-induced mortality of young sea-caught jack mackerel, Trachurus symetricus, determined with histological and morphological methods. Fish. Bull., U.S.

Theilhacker, G.H., Kimball, A.S. and Trimmer, J.S. 1986. Use of ELISPOT immunoassay to detect euphasid predation on larval anchovy. Mar Ecol. Prog. Ser. 30: 127-131.

Valenzuela, G., J. Alheit, S.H. Coombs and R. Knust. 1991 Spawning patterns of sprat and survival chances of sprat larvae in relation to frontal systems in the German Bight.
ICES C.M.1991/L:45

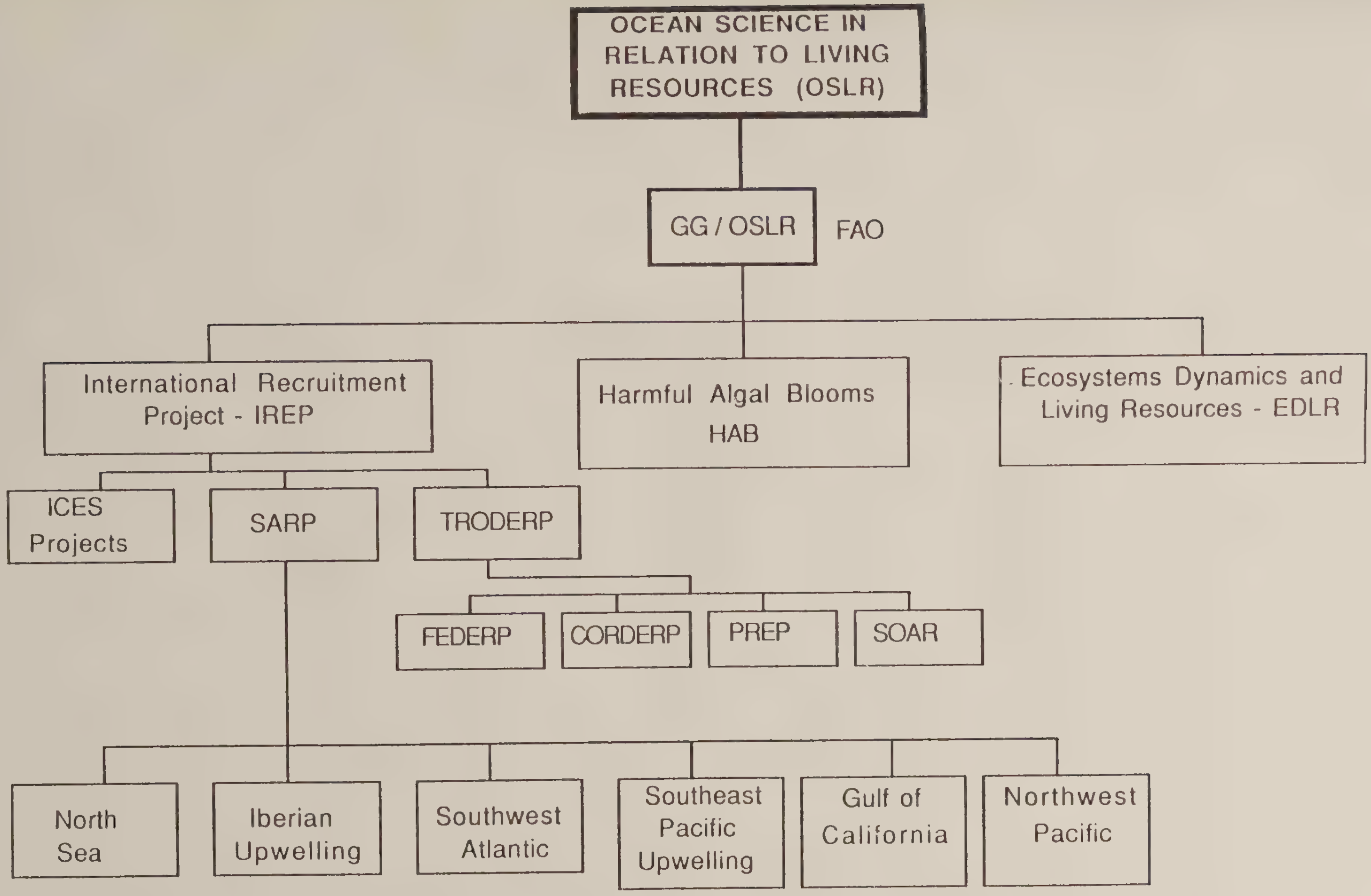
OCEAN SCIENCE IN RELATION TO LIVING RESOURCES (OSLR)
GG / OSLR
FAO
International Recruitment Project - IREP
Harmful Algal Blooms HAB
Ecosystems Dynamics and Living Resources - EDLR
ICES Projects
SARP
TRODERP
FEDERP
CORDERP
PREP
SOAR
North Sea
Iberian Upwelling
Southwest Atlantic
Southeast Pacific Upwelling
Gulf of California
Northwest Pacific

Fig.1 OSLR and its components

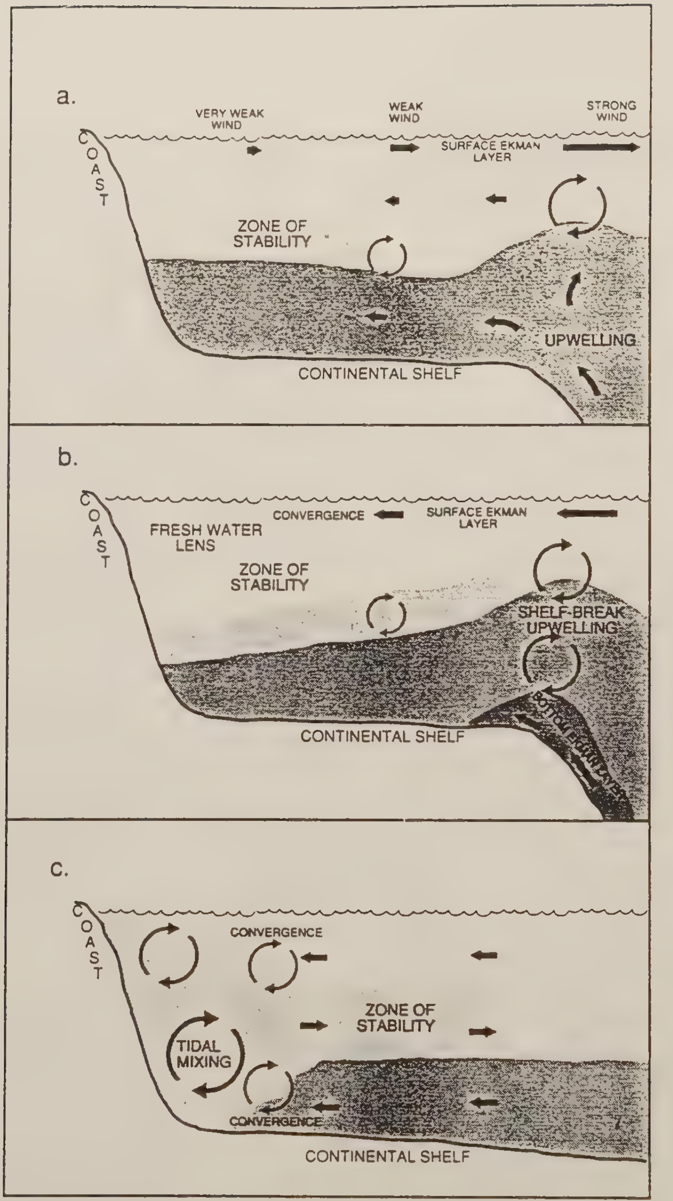
a.
VERY WEAK WIND
WEAK WIND
STRONG WIND
COAST
SURFACE EKMAN LAYER
ZONE OF STABILITY
UPWELLING
CONTINENTAL SHELF
b.
COAST
CONVERGENCE
SURFACE EKMAN LAYER
FRESH WATER LENS
ZONE OF STABILITY
SHELF-BREAK UPWELLING
BOTTOM EKMAN LAYER
CONTINENTAL SHELF
c.
COAST
CONVERGENCE
TIDAL MIXING
ZONE OF STABILITY
CONVERGENCE
CONTINENTAL SHELF

Figure 2. Schematic diagrams of environmental configurations prominent in reproductive strategies of *Engraulis anchoita*. Heavier shading connotes greater water density. Wider arrows indicate mean water transport; lengths are scaled to suggest relative magnitudes. Linked circlular pairs of arrows indicate mixing processes; their sizes are scaled to suggest relative intensities of mixing: (a) Within a coastal indentation in a wind-driven coastal upwelling regime (i.e., the Brazilian Bight; also descriptive of the Southern California Bight in the northeastern Pacific and other eastern ocean anchovy habitats.). (b) Onshore wind-driven transport over a wide continental shelf with upwelling at the shelf break and fresh water runoff rom the continent (i.e., extreme north coast of Argentina, coast of Uruguay and Brazilian coast to north of Rio Grande). (c) A shelf-sea front system driven by tidal mixing (i.e., the Patagonian shelf in the vicinity of Península Valdés; also descriptive of similar frontal systems in the North Sea, the Gulf of Maine, etc.).

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The Seasonal Cycle of Wind-Stress Curl in Subtropical Eastern Boundary Current Regions

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ABSTRACT

Historical surface marine wind reports have been processed to define characteristic seasonal distributions of wind-stress curl over the four major eastern boundary current regions of the World Ocean (i.e., the California, Canary, Benguela, and Peru/Humboldt systems) on smaller scales than previously available. Interregional comparisons show that these "classical" coastal upwelling systems are characterized by cyclonic wind-stress curl near the continental boundaries and anticyclonic curl offshore, in association with predominantly equatorward (upwelling favorable) alongshore wind stress. The cross-shore profile of alongshore stress typically has an offshore maximum located some 200 to 300 km from the coast. The decay of the wind stress toward the coast defines a region of cyclonic wind-stress curl, where coastal upwelling is enhanced by curl-induced oceanic upwelling (Ekman pumping). During summer in the respective hemispheres, the region of cyclonic curl expands poleward in each boundary current system. Particularly intense cyclonic curl occurs adjacent to capes during summer coastal upwelling maxima. During fall and winter when the upwelling system weakens, the latitudinal extent of cyclonic curl adjacent to the coast contracts, and the most intense cyclonic curl is usually associated with coastal bights.

1. Introduction

The curl of the wind stress acting on the sea surface is a fundamental forcing agent for dynamic ocean processes. It stands out as the external input term in ocean model formulations expressed in terms of vorticity balance. The same process, when considered from the viewpoint of vertical structure in the flow field, appears as the divergence of surface Ekman transport. Wind-stress curl thus controls "Ekman pumping" and associated vertical advection in regions seaward of the immediate effects of coastal boundaries (Yoshida 1955a; Yoshida and Mao 1957; Smith 1968) and so may have a variety of physical, chemical, and biological consequences to the ocean ecosystem. Potential mechanisms include rearrangements of the mass field and corresponding changes in the current structure (Yoshida 1955b), generation of baroclinic Rossby waves (White 1985; Cummins et al. 1986), and other significant contributions to variability in the coastal ocean on shorter space and time scales (Carton and Philander 1984; Brink et al. 1987; Rienecker et al. 1987). In addition, various models of eastern ocean boundary current dynamics (e.g., Hurlburt and Thompson 1973; Pedlosky 1974; McCreary et al. 1987) feature cyclonic wind-stress curl near the coast as a contributing factor for poleward undercurrents, and a suggestive correspondence between cyclonic wind-stress curl near the coast in the California Current System and the presence of eastern boundary poleward coastal counterflows has been pointed out (Munk 1950; Nelson 1977; Hickey 1979). In addition to such dynamical effects, the vertical transfers of physical and chemical properties associated with Ekman pumping can also have major effects on the biological system (Chelton 1982; Peláez and McGowan 1986; Abbott and Zion 1987).

No actual measurements of wind-stress curl are available except in rare instances where arrays of research ships or buoys have been used to make coordinated wind measurements (e.g., Halpern 1976; Düing et al. 1980) or when scatterometer data have been analyzed to construct wind-stress fields (e.g., Perigaud et al. 1989). Synoptic samplings of maritime reports may adequately define very large-scale variations (e.g., thousands of kilometers) in the wind-stress curl patterns (Willebrand 1978; Chelton 1980), but not the intermediate scales (tens to hundreds of kilometers) on which important ocean responses and biological effects are expected to occur.

Early descriptions of wind-stress curl over the ocean focused on ocean basin scales. Saunders (1976) demonstrated the effects of grid size on calculations of wind-

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stress curl and suggested that large-scale calculations underestimate the curl magnitude. Efforts to resolve mesoscale details either have involved improvements in grid resolution (Wyrtki and Meyers 1976; Hastenrath and Lamb 1977; Goldenberg and O'Brien 1981; Hellerman and Rosenstein 1983; Rienecker and Ehret 1988) or have relied on smooth curvilinear interpolations of the larger scale (Roden 1972; Evenson and Veronis 1975).

The finest-scale distributions of wind-stress curl that have been published are Nelson's (1977) mean monthly charts for the California Current region. Nelson's computational grid contains intersections at 1° latitude/longitude intervals, each intersection being the center of a 1° × 1° square area. His curl calculation employs central difference derivatives that span three grid intersections in both the zonal and meridional directions, thereby incorporating data over spans of 3° of both latitude and longitude for each computed value of the curl. The distance scale for the derivative is fixed at 2° latitude or longitude (Fig. 1a).

In this study, we further refine the scale of the curl computation (1° rather than 2° scale for the finite-difference derivatives) for the California Current System and also expand coverage to the three other "classical" subtropical eastern boundary current systems (Wooster and Reid 1963): the Canary, Benguela, and Peru/Humboldt Current systems (Fig. 2). An additional first-order correction for nonuniform distribution of reports within a given 1° × 1° square summary area is also added by adjusting for the differences between the mean latitude and longitude of the reports and the geographic center of the summary area. This avoids the possibility of grossly erroneous wind-stress curl magnitudes in cases where reports may be concentrated along narrow shipping lanes, which may not cross near the center of the 1° × 1° square.

To produce these distributions, maritime data from a large number of years are composited together to yield mean wind-stress patterns on much finer scales than are definable in synoptic samples of these data. Interannual variability is suppressed by compositing many years together, revealing characteristic seasonalities. As shown below, the curl is a linear mathematical operator and therefore the field of curl of the mean wind stress will, as sampling error decreases, tend increasingly to resemble the true mean field of the curl of the wind stress.

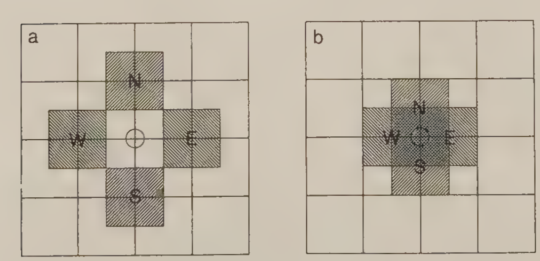


FIG. 1. Computational grids used for wind-stress curl calculations. Grid intersections are spaced 1° latitude by 1° longitude apart. (a) The central difference scheme of Nelson (1977) yields a 2° length scale for the derivatives. (b) The staggered grid used in this study in which 1° × 1° summary areas for the separate wind-stress components overlap allows a 1° length scale for the finite-difference computations.

These higher resolution distributions are intended to serve as checks for possible scale-related artifacts in Nelson's (1977) results for the California Current region. Corresponding distributions for the eastern boundary current regions of the North and South Atlantic oceans, and of the South Pacific Ocean, are intended to provide indications of the generality of the various features and to constitute a basis for applying the "comparative method" (e.g., Bakun and Parrish 1990) to classify and interpret similar characteristics in the wind-stress curl patterns among the four regions, and to draw conclusions as to their dynamical and ecological significances.

2. Methods

a. Data processing and computation procedures

Ship wind reports were extracted from the NOAA National Climatic Data Center's (NCDC) global file of surface marine observations (Tape Data Family-11). A single-pass editor was used to ensure physically possible values and to remove other gross errors in the data, including obviously erroneous position reports and wind observations exceeding extreme magnitude limits.

The stress estimates are computed from individual wind reports according to the bulk aerodynamic formula

$$\tau = \rho C_d |\mathbf{V}| \mathbf{V}, \qquad (1)$$

where τ is the stress vector, ρ is the density of air, C_d is a dimensionless drag coefficient, $\mathbf{V}$ is the wind velocity, and $|\mathbf{V}|$ is the wind speed. Following Nelson (1977), the parameters C_d and ρ are held constant (0.0013 and 0.00122 g cm^{-3}).

Summary grids of one-degree latitude/longitude areal quadrangles were set along the mainly meridional portions of the continental boundaries of the four regions (Fig. 2), so as to cover the generally equatorward eastern boundary current flows and the associated temperate coastal upwelling systems. In each region the summary grid roughly parallels the coastline configuration and extends from the coast to between 11° and 15° longitude offshore. The scale of the curl computation is minimized, while maintaining a 1° × 1° areal sample size for each mean stress component estimate by employing a "staggered" grid arrangement in which the grids for the respective zonal and meridional wind stress component summaries are offset from one another by 0.5° in both latitude and longitude

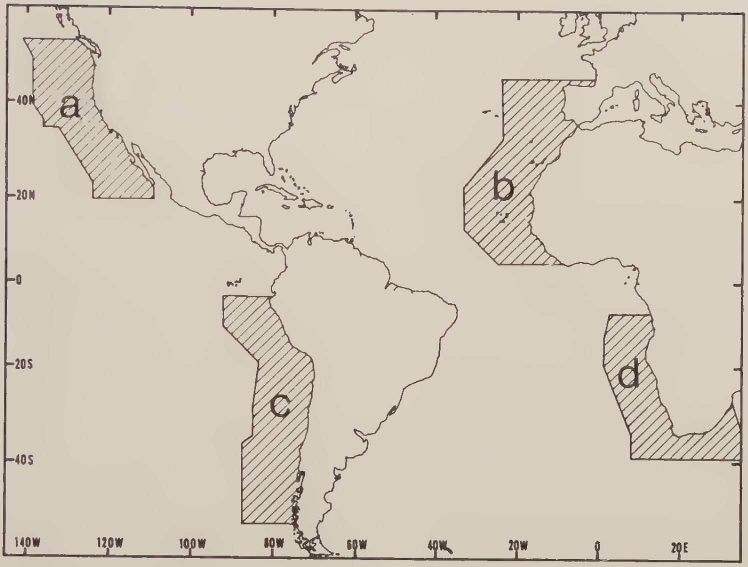


FIG. 2. Subtropical eastern boundary current domains for which wind-stress curl distributions are mapped in Figs. 7–10. (a) California Current region, (b) Canary Current region, (c), Peru/Humboldt Current region, and (d) Benguela Current region.

(Fig. 1b). Long-term composite seasonal distributions were constructed by averaging all available data within each 1° × 1° square over each of six 2-month segments of the annual cycle.

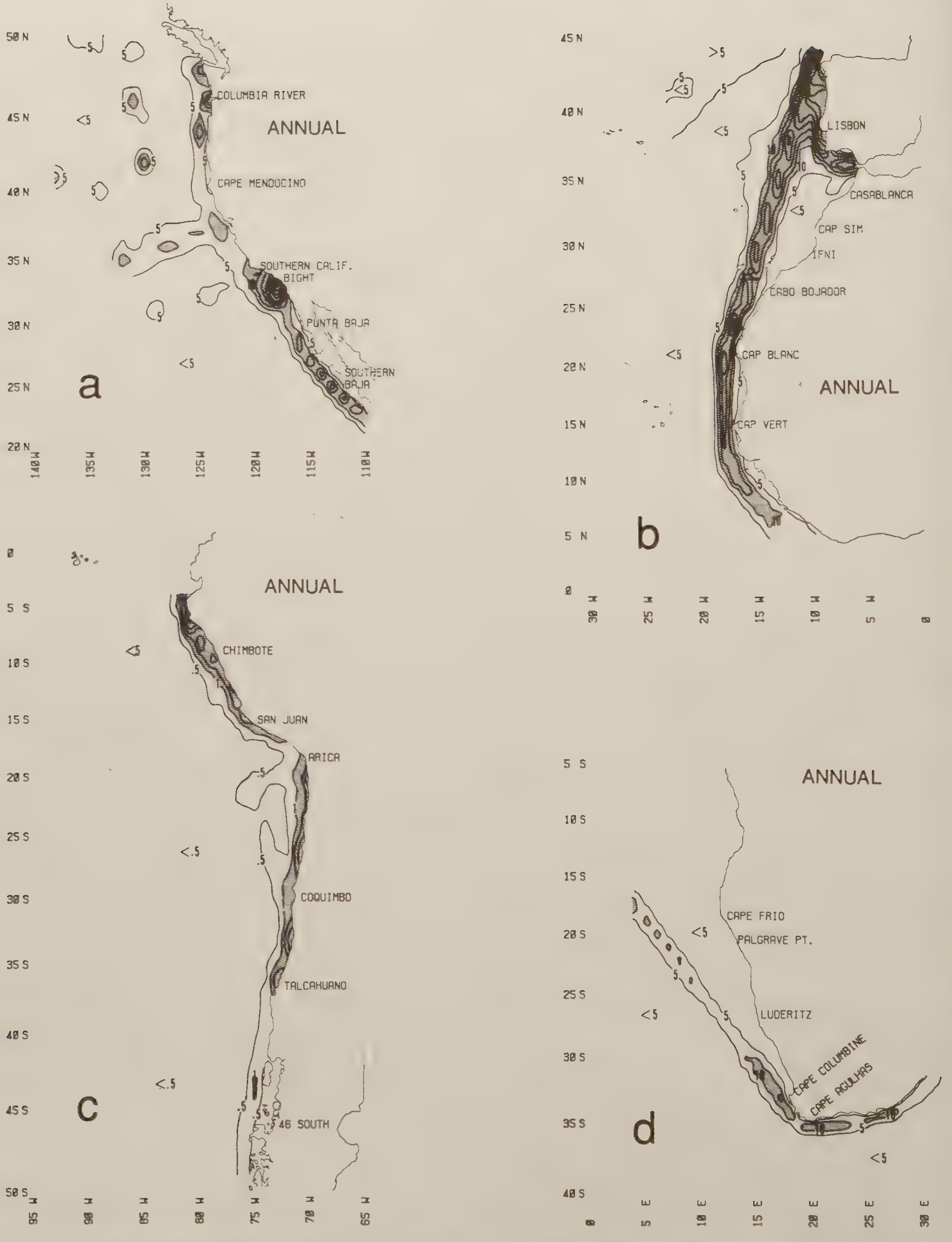
Available data density is highly variable among regions and within regions (Fig. 3). The version of the data file used contains data extending from the nineteenth century through 1979. Total numbers of observations range from fewer than 0.3 million reports in the Peru/Humboldt Current region to more than 3.3 million reports for the Canary Current system. Individual 1° × 1° areal samples contain less than 50 observations for the entire period in some regions off Peru and Chile, but in excess of 40 000 observations in portions of the Southern California Bight and off the Iberian Peninsula. The highest density of reports lies within 300 km of each coast, along the primary shipping routes, except off southwestern Africa, where the narrow, transoceanic shipping lane diverges from the coast (Fig. 3d).

Prior to 1950, a large percentage of the available maritime reports contain positions reported only to the nearest whole degree of latitude and longitude. These reports are not amenable to the staggered grid computation scheme in which the samples of the respective wind-stress components are offset by 0.5° in each coordinate direction. Accordingly, the 30-year period, 1950–79, has been chosen as the basic time frame for compositing data to construct the wind stress and wind-stress curl fields. One deviation from this procedure was required to construct the distributions for the Peru/Humboldt Current region where data density is an order of magnitude lower than the other three regions (Fig. 3). Because of the extremely undersampled nature of the distributions, it was deemed necessary to relax our procedures somewhat for much of the Peru/Humboldt Current region to incorporate all the available data in the historical record (1850–1979). For the major portion of that particular region, older data with positions that may have been reported only to whole degrees of latitude and longitude were treated as if they were actually accurately positioned at the integral 1° latitude/longitude intersections. Each of the 2-month, seasonal wind-stress curl distributions for the Peru/Humboldt Current region is based on approximately one-sixth of the total available data density depicted in Fig. 3c. For the California, Canary, and Benguela current systems, the data density reflected in these computations is reduced by an additional factor of approximately one-half because only data since 1950 have been used for these three regions.

In spherical coordinates, the vertical component of the curl of the wind stress on the sea surface, $\mathbf{k}\cdot\nabla\times\boldsymbol{\tau}$, is calculated as

$$\mathbf{k}\cdot\nabla\times\boldsymbol{\tau} = \frac{1}{R\cos\phi}\left[\frac{\partial\tau_\phi}{\partial\lambda} - \frac{\partial(\tau_\lambda\cos\phi)}{\partial\phi}\right], \qquad (2)$$

where R is the mean radius of the earth, ϕ and λ are the latitude and longitude (in radians), and $\partial\tau_\phi/\partial\lambda$ and $\partial(\tau_\lambda\cos\phi)/\partial\phi$ are the zonal derivative of merid-


a
ANNUAL
50 N
45 N
40 N
35 N
30 N
25 N
20 N
140 W
135 W
130 W
125 W
120 W
115 W
110 W
COLUMBIA RIVER
CAPE MENDOCINO
SOUTHERN CALIF. BIGHT
PUNTA BAJA
SOUTHERN BAJA
<5
5
b
ANNUAL
45 N
40 N
35 N
30 N
25 N
20 N
15 N
10 N
5 N
0
30 W
25 W
20 W
15 W
10 W
5 W
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LISBON
CASABLANCA
CAP SIM
IFNI
CABO BOJADOR
CAP BLANC
CAP VERT
>5
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40 S
45 S
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90 W
85 W
80 W
75 W
70 W
65 W
CHIMBOTE
SAN JUAN
ARICA
COQUIMBO
TALCAHUANO
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0
5 E
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CAPE FRIO
PALGRAVE PT.
LUDERITZ
CAPE COLUMBINE
CAPE AGULHAS
<5
5

FIG. 3. Distribution of observations ($\times 10^3$) per 1° × 1° quadrangle in the four eastern boundary current regions for the period extending from the late nineteenth century through 1979. (a) California Current region, (b) Canary Current region, (c) Peru/Humboldt Current region, and (d) Benguela Current region. Contour interval is 5000 and values greater than 10 000 observations per 1° × 1° box are shaded in (a), (b), and (d). Contour interval is 500 and values greater than 1000 observations per 1° × 1° box are shaded in (c).

ional stress and the meridional derivative of zonal stress, respectively.

The finite difference form of (2) is

$$\mathbf{k}\cdot\nabla\times\boldsymbol{\tau} = \frac{1}{R\cos\phi}\left[\frac{\tau_{\phi(E)}-\tau_{\phi(W)}}{\Delta\lambda} - \frac{\tau_{\lambda(N)}\cos\phi(N)-\tau_{\lambda(S)}\cos\phi(S)}{\Delta\phi}\right], \quad (3)$$

where $\tau_{\phi(E)}$, $\tau_{\phi(W)}$, $\tau_{\lambda(N)}$, and $\tau_{\lambda(S)}$ are the averages of the wind-stress component estimates in the four 1° × 1° summary areas involved in a given calculation (Fig. 1b), and $\Delta\lambda$ and $\Delta\phi$ are the differences in the mean longitudes in the two areal segments involved in the zonal derivative and the mean latitudes in the two areal segments involved in the meridional derivative, respectively.

To estimate sampling error, the characteristic long-term seasonal wind stress distributions are considered to be sufficiently well sampled for the standard error of the mean to provide a reasonable estimate of error. Accordingly, the variances of the 1° × 1° stress component samples are carried through the curl calculation following standard procedures (Beers 1953), that is,

$$\sigma^2_{\text{curl}} = \frac{1}{R\cos\phi}\left[\frac{\sigma^2_{\tau_{\phi(E)}}+\sigma^2_{\tau_{\phi(W)}}}{\Delta\lambda} + \frac{\cos^2\phi(N)\,\sigma^2_{\tau_{\lambda(N)}}+\cos^2\phi(S)\,\sigma^2_{\tau_{\lambda(S)}}}{\Delta\phi}\right], \quad (4)$$

where σ^2_{curl} represents the variance of the curl estimate, and $\sigma^2_{\tau_{\phi(E)}}$, $\sigma^2_{\tau_{\phi(W)}}$, $\sigma^2_{\tau_{\lambda(N)}}$, and $\sigma^2_{\tau_{\lambda(S)}}$ represent the variances of the estimates of the stress components appearing in (3).

b. Error analysis

Various errors may introduce uncertainties into the quantities appearing in (3). These errors may be classified as being either systematic or random (Weare 1989). Systematic error that might be due to inadequacy of the bulk formulation approach itself is hard to assess (Hsiung 1986). Direct sea surface stress measurements are difficult and there is large scatter in the results. Certainly, systematic direct measurements of wind stress have not been made under all ocean conditions, various proximities to coastal features, and other possible effects that occur within the areas addressed in this study.

The most obvious uncertainty of the systematic type is the use of a constant drag coefficient, C_d, in the stress computation (1). It seems clear that the value of C_d is dependent on both wind speed and atmospheric stability (Large and Pond 1981; Blanc 1985; Smith 1988; Trenberth et al. 1989). However, there is no universally adopted variable formulation for C_d at the present time, and research on the problem is a continuing activity. Because of this, it has become common to avoid this particular issue by computing a quantity called the pseudostress (Goldenberg and O'Brien 1981; Servain and Legler 1986; Breidenbach 1990), which is the stress divided by ρC_d (i.e., a vector with magnitude equal to the wind speed squared and having the same direction as the wind velocity).

One important use of the distributions we have produced will be in applications of the comparative method (Bakun and Parrish 1990) to draw inferences concerning important scales that are not amenable to experiments or directed observational programs. By retaining a constant factor for ρC_d, our results are equivalent to results expressed in terms of pseudostress, but scaled so as to carry actual stress units and to reflect reasonable magnitudes with respect to those units. This particular constant factor serves to make our results directly comparable with results of Nelson (1977), Wooster et al. (1976), Bakun (1978), Parrish et al. (1983), Bakun and Parrish (1990), Bakun (1990), and various other studies that have employed an identical formulation. Similarly, they can be readily made comparable to any of the many other studies using constant coefficient formulations by simple multiplication by an appropriate ratio of the constant factors.

Magnitudes of wind stress computed according to our constant factor formulation and a formulation presented by Large and Pond (1981), which includes wind-speed dependence are compared in Fig. 4. Wind-speed distributions in subtropical eastern ocean boundary regions tend to have a mode near 5–7 m s^{-1} and contain relatively few observations exceeding 14 m s^{-1} (Nelson 1977). In this range, the two formulations (Fig. 4) yield very similar stress estimates. Thus, the constant and wind-speed–dependent drag coefficient formulations should not produce widely differing long-term averages.

With regard to the effect of atmospheric stability, it has been previously demonstrated for similar one-degree summaries in the California Current region (Nelson 1977), and on larger scales for all four regions

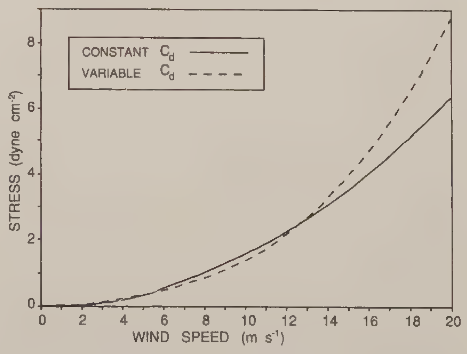


FIG. 4. Comparison of stresses computed with constant and wind-speed-dependent drag coefficient formulations.

(Hellerman and Rosenstein 1983), that the effect of stability on averages of computed stresses in eastern boundary regions is only of the order of several hundredths of a dyn cm^{-2}. There also seems to be little significant spatial pattern in the stability effect that could substantially affect derived wind-stress curl distributions. One exception indicated by Hellerman and Rosenstein (1983) is an area directly off the southern tip of Africa, where neglect of the effect of atmospheric stability may lead to an underestimate of the order of 0.1 dyn cm^{-2}. The bulk of the available wind reports in the pre-1980s historical files are Beaufort estimates rather than anemometer measurements. These estimates, which are based on visual effects of winds on the sea surface, are "raised" to reflect a 10-m "mast height" reference using conversion tables that largely assume a neutral stability profile. In transferring what was originally sea surface information from the 10-m reference height down to the sea surface level at which the stress is determined, it seems appropriate to adhere to the same assumption. In regard to air density, ρ, any effect of a constant value in the stress computation will be small in these regions, where the airflow is generally from the ocean toward the continent and where effects of upwelling and advection tend to damp the seasonal temperature cycle.

The fraction of anemometer measurements in the marine report files has been increasing over recent decades (Ramage 1987). It appears that the majority of ship anemometers are actually installed at greater heights above the sea surface than the 10-m standard height to which the Beaufort estimates and bulk stress formulas are calibrated (Cardone et al. 1990). This would cause an overestimate of the wind at 10 m, which would lead to a corresponding overestimate of the sea surface stress. Thus, there may be an artificial increasing trend in wind speeds inferred from the maritime data files. However, such a trend should not affect the spatial pattern in long-term averages of wind stress and wind-stress curl, unless there were spatial patterns in the trend. Although the proportion of anemometer-based reports appears to have increased more rapidly in the Pacific than in the Atlantic, there is no reason to suspect spatial pattern in the trend within regions.

The Beaufort wind estimates themselves may have systematic errors. The British (e.g., Shearman 1983) apparently prefer the Beaufort estimate over actual wind measurements because the sea state reflects an integration of the wind effects over about an hour, whereas measured winds reflect a much more instantaneous description. However, Böning et al. (1991) indicate that the official World Meteorological Organization (WMO) conversion scale for Beaufort estimates systematically underestimates low wind speeds and overestimates high wind speeds. Isemer and Hasse (1991) demonstrate that the effect on the climatological wind-stress curl distribution could be substantial, resulting in as much as a 30% underestimate of total Sverdrup transport integrated westward across the North Atlantic Ocean from the eastern boundary.

In summary, there are several possible sources of systematic error in the quantities used in the stress computation. Of those for which it is possible to guess a probable tendency for bias, the lack of a wind speed dependence in the drag coefficient would seem to lead, if anything, to an underestimate because of suppression of the effect of particularly high wind speeds, as would the effect of errors in the WMO–Beaufort conversion scale. The effect of anemometer measurements would be toward an overestimate. Because of the nonlinearity in the stress computation (1), quasi-random error variance in the wind observations will itself lead to some degree of systematic overestimate of the average stress (e.g., an error of increased wind speed will make more contribution to the average stress than an equal error of reduced wind speed). Thus, at least some of the different sources of systematic error would seem to counteract one another to some degree.

In any case, on the small scales of these computations, the true long-term mean, spatially adjacent stress vectors must be largely codirectional. Therefore, systematic uncertainties will tend to be in the same sense in adjacent samples and thus to be somewhat self-canceling in the subtractions involved in forming the finite-difference derivatives in (3). They will produce generally equivalent percentage uncertainties in the curl magnitudes to those produced in the stress magnitudes (i.e., perhaps from a few percent to certainly not more than 10 to 20 percent). It is well known that the magnitude of sea surface wind-stress curl is highly scale dependent in any case (e.g., Saunders 1976; Hellerman and Rosenstein 1983). In this study we are interested in spatial pattern in the wind-stress curl field (e.g., the locations of maxima, minima, strong gradients, the "zero-curl contour" where the sea surface Ekman transport field changes from convergent to divergent, etc.). These aspects should not be substantially affected by systematic errors.

A much greater problem than systematic errors (particularly to a study like ours where the focus is on mesoscale pattern rather than on integrated ocean basin-scale effects) is the more random type of error inherent in marine weather reports. These include imprecision and mistakes in the observations, but also errors in recording of the data in logbooks and in the manual extraction and redigitization process. For example, a not uncommon error occurs in coding the correct hemisphere for the geographical position (one can see this in global maps of maritime report positions in which, when a long enough period to assemble sufficient numbers of reports is incorporated, "reflections" of major shipping routes located in an opposite hemisphere may appear to traverse land areas, ocean areas of particularly low report densities, etc.). Clearly, this can be a serious problem where, for example, a few observations taken during the winter season from heavily sampled areas near the U.S. East Coast, north of Cape Hatteras could erroneously reflect across the equator to appear in an extremely sparsely sampled (Fig. 3) summer situation near the Chilean coast, south of Talcahuano. Likewise, observations from within the Mediterranean Sea might erroneously reflect into data poor offshore regions off southern Africa, and observations near Hong Kong Harbor might reflect across the Greenwich meridian to appear in the data poor areas offshore of southern Baja California.

These errors combine with real natural variability to produce large variances in the wind sample distributions. These are, in turn, amplified in the nonlinear stress calculation (1) and again in the differencing operations involved in the curl computation (3). This results in very "noisy" distributions of one-degree wind-stress curl estimates, carrying large and variable standard error estimates computed according to (4). The wide scatter of standard error estimates in the subsample illustrated in Fig. 5 is typical. Comparisons among differently constituted subsamples indicate some degree of dependence on season, with winter seasons yielding slightly higher average standard errors than summer, and a larger degree of dependence on latitude (for example, "smoothed" values of the standard errors tend to be about 25% less in samples of the latitude band from 9° to 19° than in samples of the band from 23° to 33°). No clear differences between the regions are apparent once the seasonal and latitudinal dependencies have been considered. As might be inferred from the latitudinal and seasonal dependencies, the standard error appears to increase with mean curl magnitude. However, the increase in standard error is slower than the increase in magnitude (Fig. 6). Thus, higher magnitudes of computed curl, while generally carrying greater standard errors, tend to be more significant than low curl magnitudes. However, as expected, both the characteristic mean level of standard error and its scatter decreases with increasing numbers of observations incorporated in the calculation (Fig. 5).

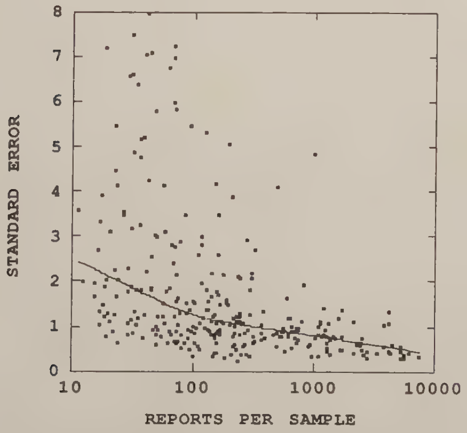


FIG. 5. Typical scatterplot of standard error calculations (1×10^{-8} dyn cm^{-3}) versus average number of observations in the four 1° areal samples used in the curl calculation. The curve was fitted to the data by robust locally weighted regression using the LOWESS method (Cleveland 1981).

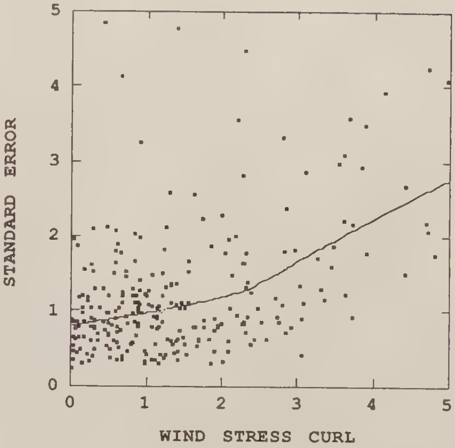
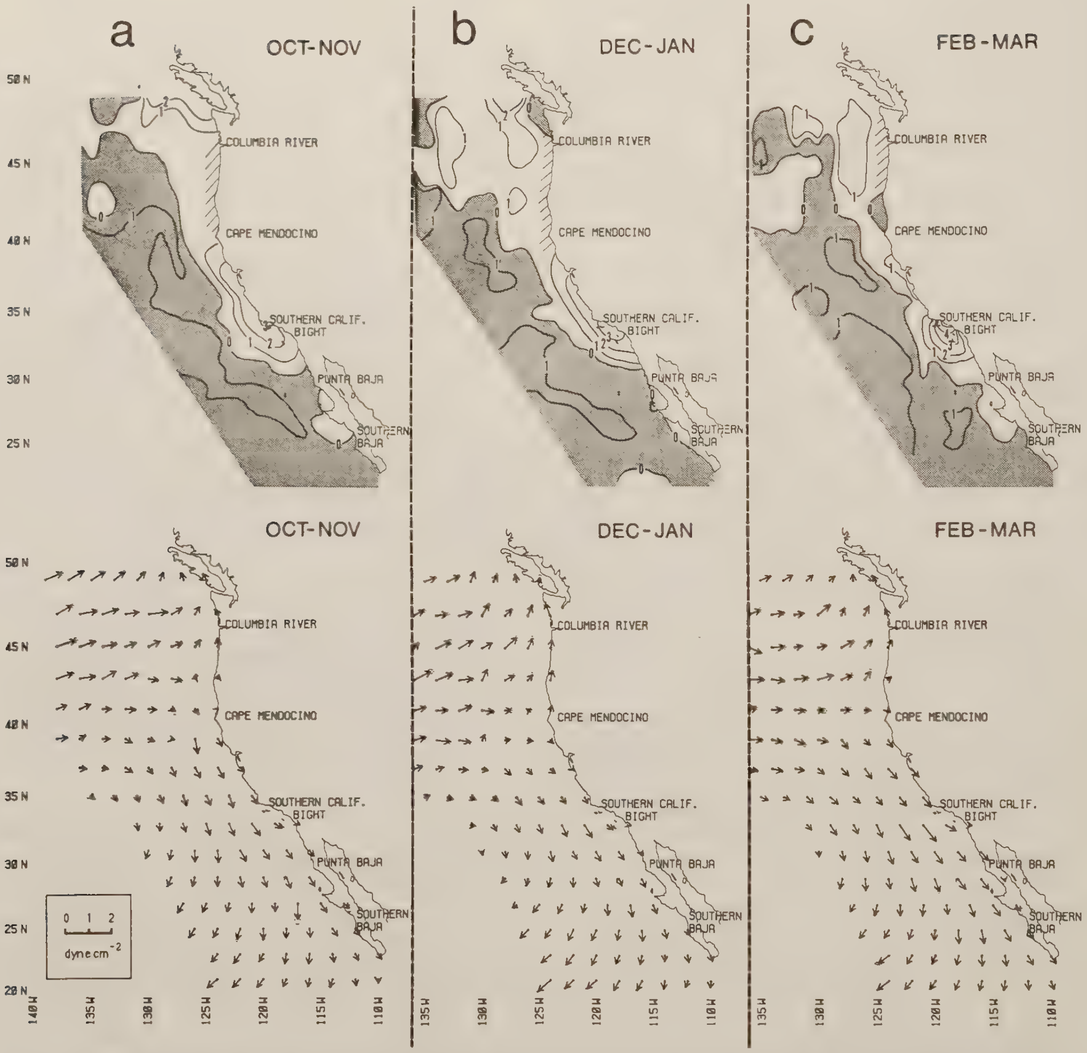


FIG. 6. Typical scatterplot of standard error calculations versus computed wind-stress curl magnitude (1×10^{-8} dyn cm^{-3}). The curve was fitted to the data by robust locally weighted regression using the LOWESS method (Cleveland 1981).

c. Construction of smoothed curl fields

In Nelson's (1977) contoured charts for the California Current region, noise was not suppressed, essentially leaving it to the viewer to determine the significant patterns, taking into account the visual indication of the noise component. However, this led to confusion among certain users, who apparently had difficulty in distinguishing real features from sampling error. In the present study, the choice was made to deal with the noise through analysis and smoothing, but to attempt to retain the finest scale of significant pattern available in any location. Of course, this varies greatly both within and among the four regions due to the geographical differences both in available data densities (Fig. 3) and in actual conditions. Accordingly, no smoothing of the stress fields was performed prior to the curl computation. Several steps, which combined both objective and subjective approaches, were taken to deal with the resulting noise component to yield significant, recognizable wind-stress curl patterns.

In addition to the 2-month segments of the seasonal cycles, which form the basic temporal unit of this study (i.e., the presentations in Figs. 7 to 10), separate independent single-month mean distributions of wind stress and wind-stress curl were also prepared and subjected to the same treatments enumerated next. These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CAPE MENDOCINO
SOUTHERN CALIF. BIGHT
PUNTA BAJA
SOUTHERN BAJA
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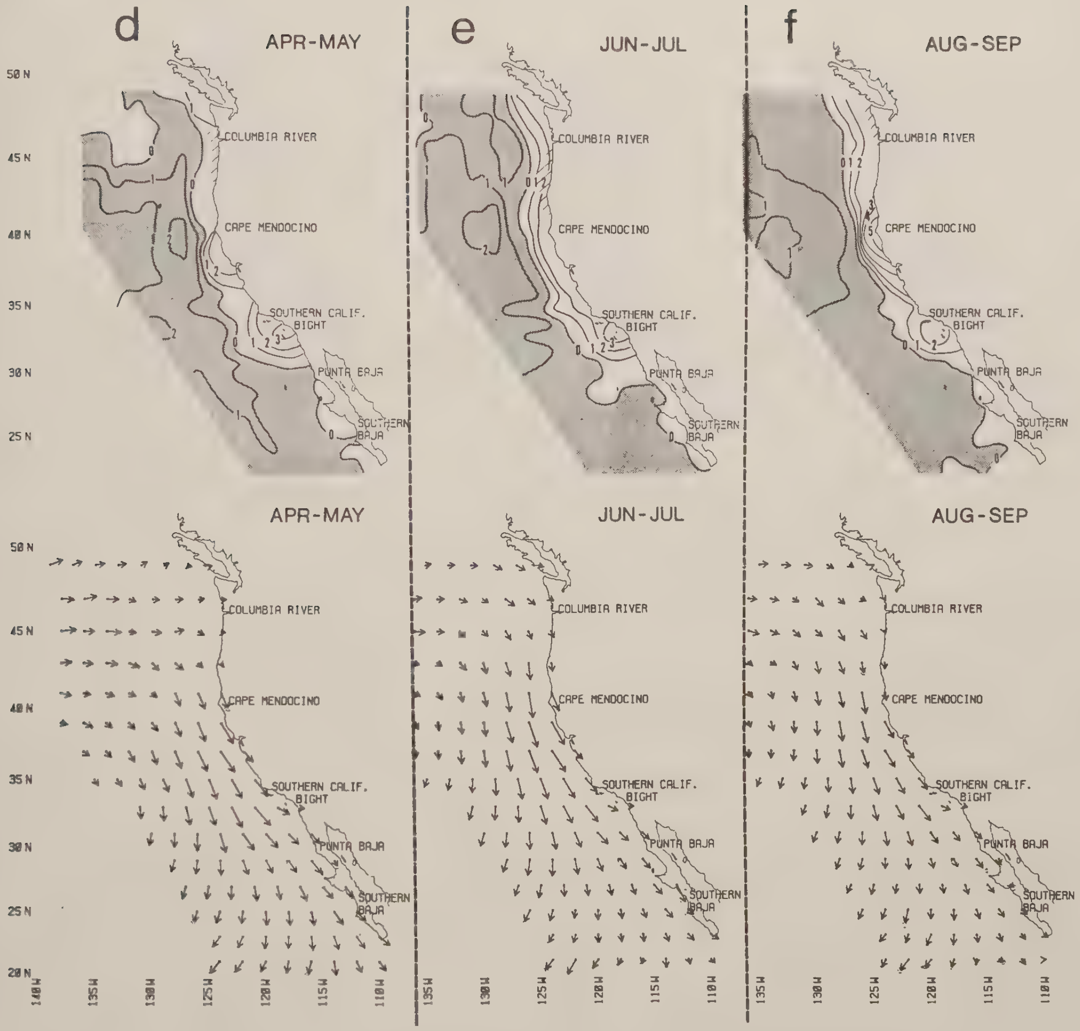
dyne cm-2
140W
135W
130W
125W
120W
115W
110W

FIG. 7. California Current region: wind-stress curl (10^{-8} dyn cm^{-3}) and surface wind stress (dyn cm^{-2}) distributions. Contour interval is 1×10^{-8} dyn cm^{-3} and regions of anticyclonic curl are shaded. Wind-stress vectors are plotted at alternate latitude and longitude intersections, and symbols are scaled according to the key on the chart. (a) October–November, (b) December–January, (c) February–March,

provided dual independent checks on wind-stress curl features within each of the 2-month seasonal segments for which composite distributions are presented. Preliminary objectively contoured maps of all the 1-month and 2-month distributions, in their original state, were prepared as a first step in the process of constructing characteristic distributions.

Companion maps of discrete symbols indicating both magnitude and standard error for each gridpoint estimate of wind-stress curl were also prepared for all the 1-month and 2-month distributions. These provided a readily referenced estimate of the reliability of each computed wind-stress curl value. Another guide to significance was provided by the degree of spatial and temporal coherence among the independent estimates (except in locations directly adjacent to prominent coastal features where spatial coherence might not be expected). That is, features that were coherently indicated on scales larger than 2° × 2° squares (because directly adjacent one-degree curl estimates share data and, so, are not independent) and in both single-month subsamples of a 2-month set were assigned high prob-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140W
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120W
115W
110W

FIG. 7. (*Continued*) (d) April–May, (e) June–July, and (f) August–September.

ability of reality. The intent was to be conservative in the subjective mapping process and to avoid defining questionable features.

Maps of spatially smoothed, 2-month wind-stress curl distributions were also prepared and objectively contoured. A nonlinear smoother was employed. The usual linear smoothing techniques were deemed inadequate in this case, as they merely spread intense bull's-eyes, which largely obscured the underlying significant patterns in the data-poor areas. Rather, a 3 × 3 gridpoint version of the nonlinear median smoother (Beaton and Tukey 1974; Rabiner et al. 1975) was employed, whereby the value at each grid location was replaced by the median of the nine values in the 3 × 3 grid segment centered at the location. The grid indexing was set up such that the zonal grid coordinate was referenced to the coastline rather than to a constant longitude. Where the coastline trend deviated from a largely meridional orientation, the 3 × 3 filter "rectangle" was distorted into somewhat of a "parallelogram" shape, with the sloping sides of the parallelogram oriented generally along the trend of the coast.

These objectively filtered maps provided a fairly smoothed, organized background. However, details that may have been lost in the filtering process, but

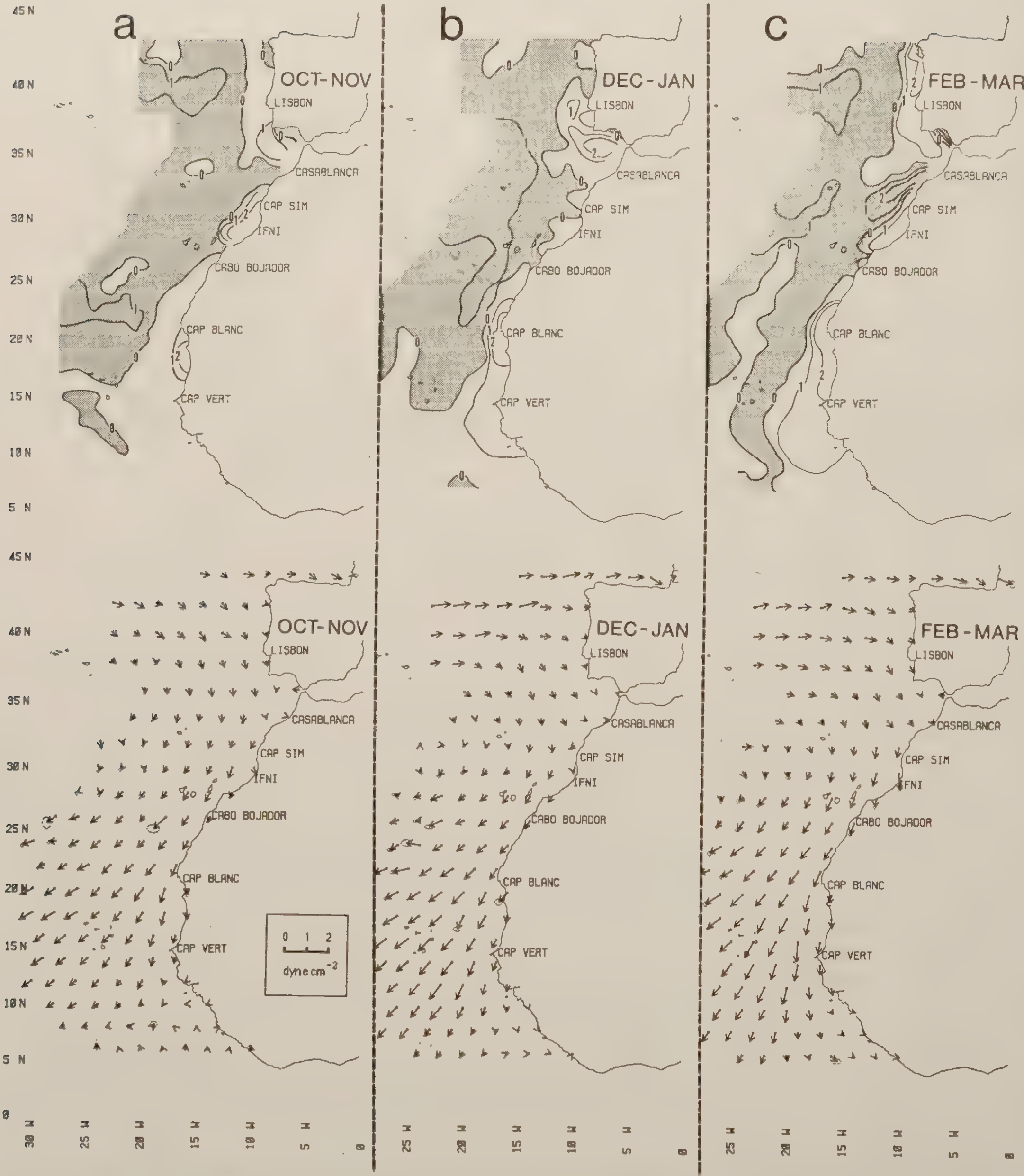
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FIG. 8. Canary Current region: wind-stress curl (10^{-8} dyn cm^{-3}) and surface wind-stress (dyn cm^{-2}) distributions. Contour interval is 1 × 10^{-8} dyn cm^{-3} and regions of anticyclonic curl are shaded. Wind-stress vectors are plotted at alternate latitude and longitude intersections, and symbols are scaled according to the key on the chart. (a) October–November, (b) December–January, (c) February–March,

were indicated as significant by the other aforementioned examinations were added by overlaying the smoothed and unsmoothed distributions and drawing the final contours, while continually referring to the 1-month subsample distributions and to the maps of discrete symbols carrying the standard error indicators as

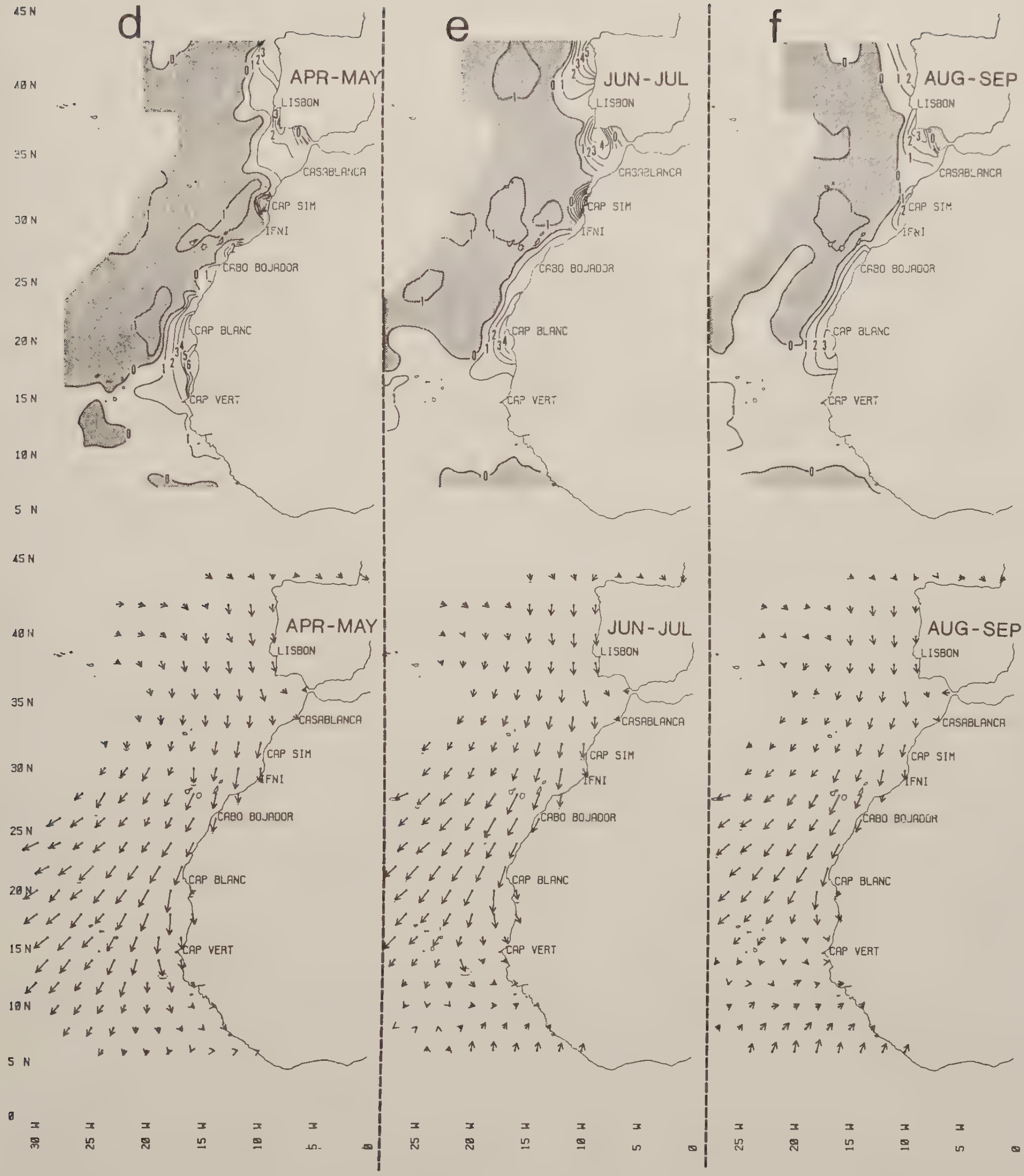
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FIG. 8. (*Continued*) (d) April–May, (e) June–July, and (f) August–September.

guides. This subjective process was necessary to extract the maximum amount of information supported by the data. The largest sampling errors were often due to a "data problem" in a particular one-degree areal sample. Because each sample contributes to two adjacent curl computations, the effect is reflected as two adjacent anomalous "spikes" of opposite sign, each carrying a very large standard error estimate. It was

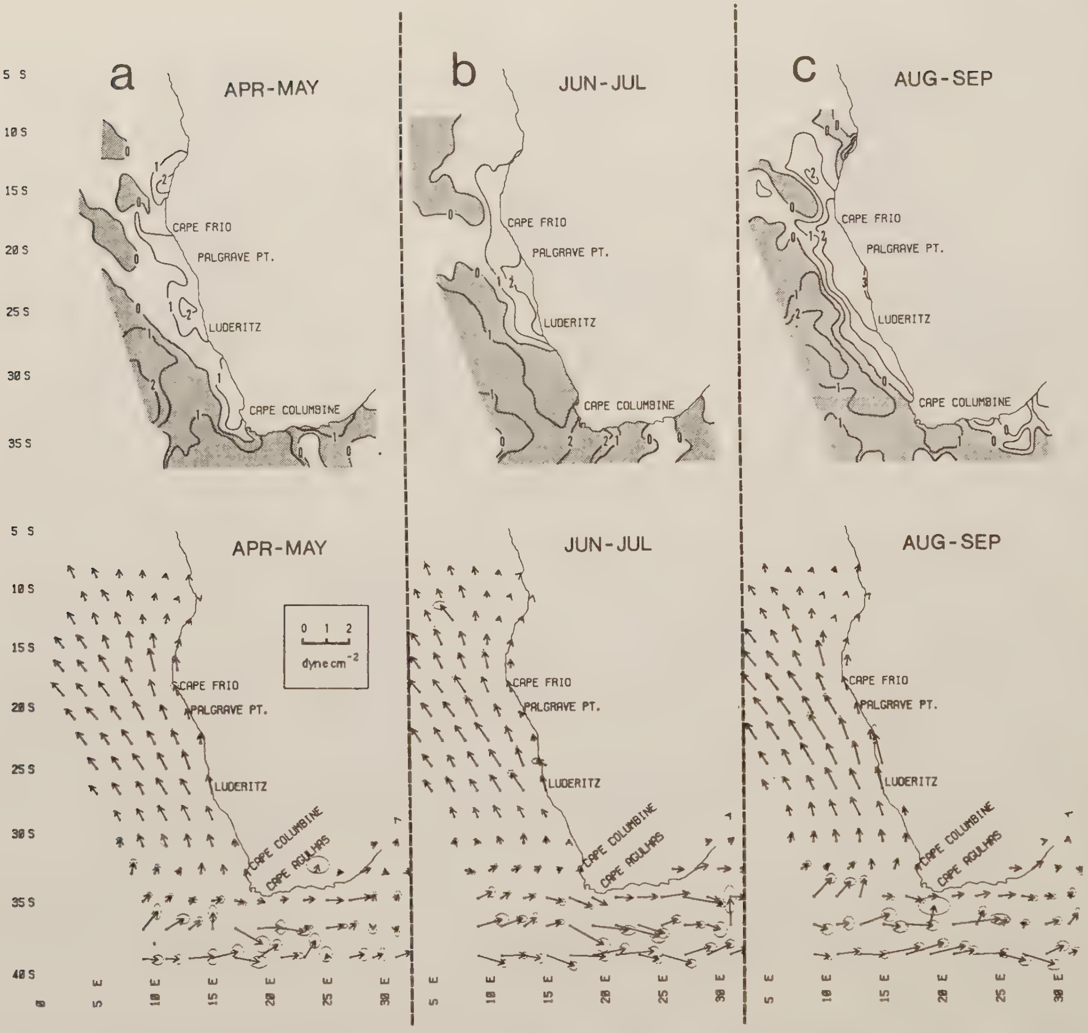


FIG. 9. Benguela Current region: wind-stress curl (10^{-8} dyn cm^{-3}) and surface wind-stress (dyn cm^{-2}) distributions. Contour interval is 1×10^{-8} dyn cm^{-3} and regions of anticyclonic curl are shaded. Wind-stress vectors are plotted at alternate latitude and longitude intersections, and symbols are scaled according to the key on the chart. (a) April–May, (b) June–July, (c) August–September,

relatively easy to recognize major errors of this type and to ensure that they were effectively removed by the smoothing and were not reinserted.

The entire process was applied independently to each 2-month sample set. No conscious transfer of information between sample sets was allowed. The six maps presented in each of Figs. 7–10 are thus based as independently from one another as possible, in spite of the subjective aspects of their construction. No "after the fact" recontouring has been performed to bring indicated features into better conformity among different maps, even when after reexamination, the data might have supported it.

To aid interpretation of the wind-stress curl distributions (Figs. 7–10), we have juxtaposed corresponding distributions of wind-stress vector symbols. Vectors are shown only at alternate grid points in both latitude and longitude to avoid clutter. Thus, the wind-stress vector maps represent only one-fourth of the total number of 1° × 1° areal samples which have been incorporated in each corresponding wind-stress curl map. No smoothing has been employed in the vector

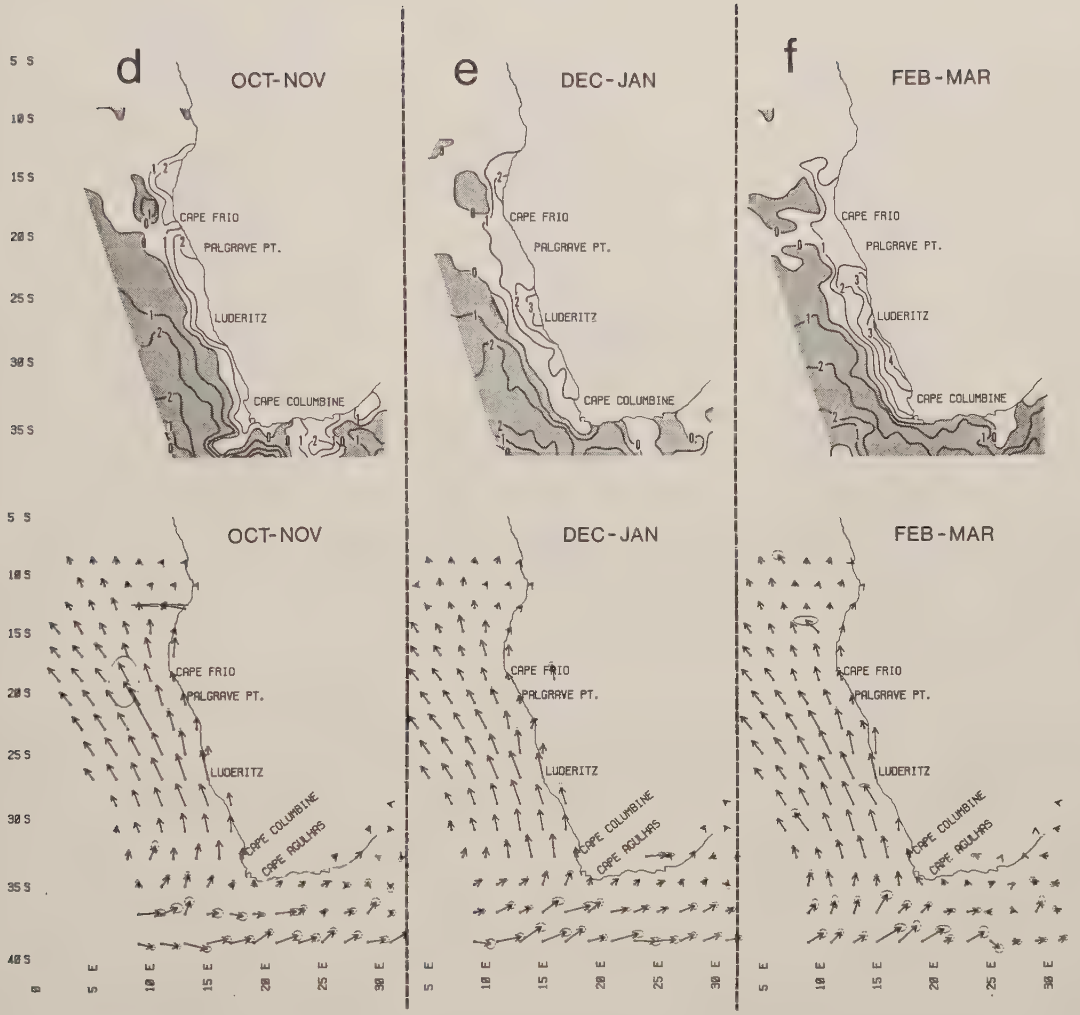
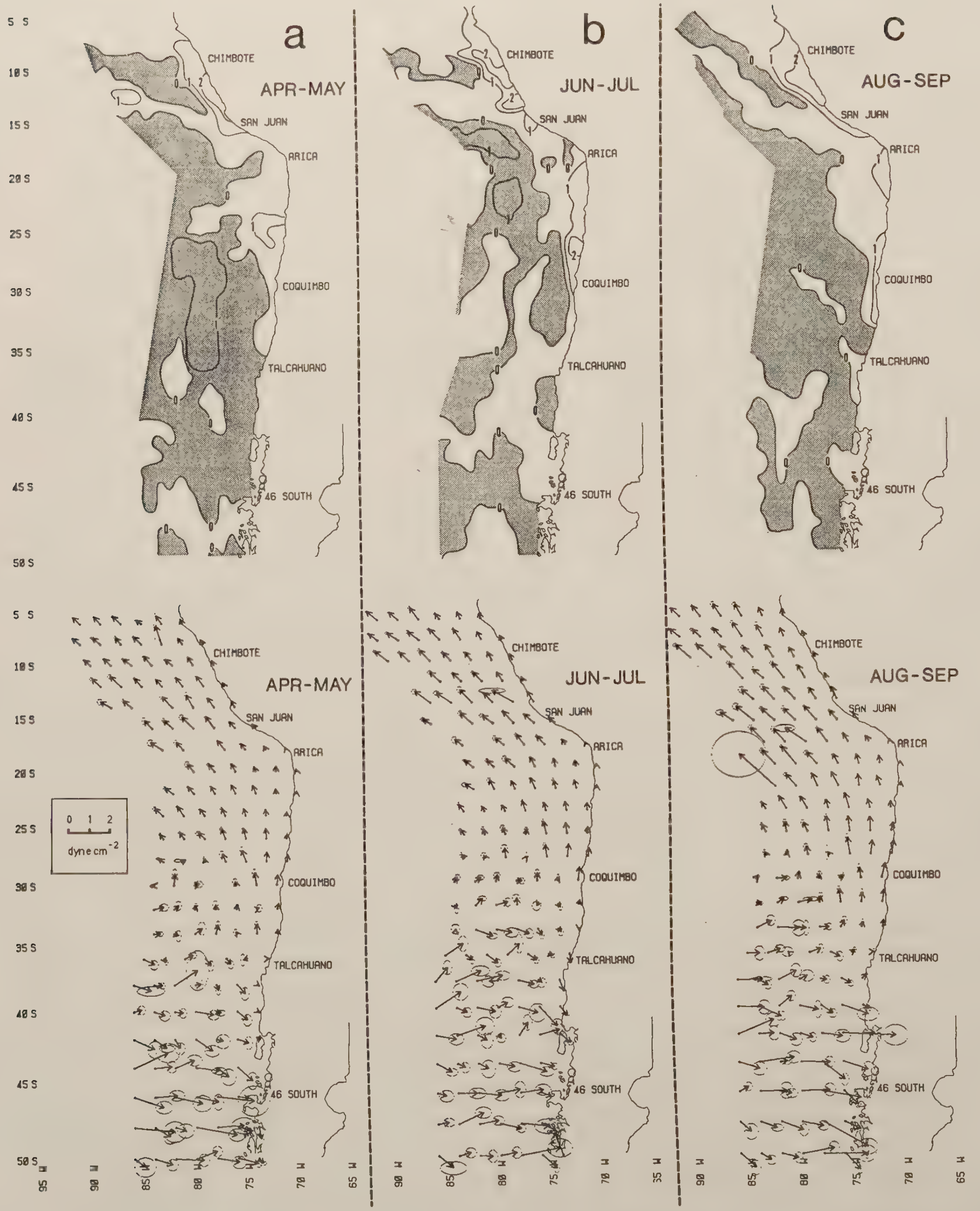


FIG. 9. (*Continued*) (d) October–November, (e) December–January, and (f) February–March.

presentations. Each vector represents a dataset that is entirely independent of any data reflected in any of the other vectors in any of the maps. The degree of coherence among the vectors in these maps provides a visual gauge to the internal consistency among independent 1° × 1° bimonthly datasets. To indicate the relative effects of sampling errors versus real small-scale differences, error ellipses, having axes defined by the standard errors of the two component means defining each vector, are outlined by fine dots at the head of each vector symbol. These error ellipses tend to be visually apparent only when the standard errors are rather large and are more obvious in the data-poor regions (e.g., Fig. 10) than in the regions where data are abundant (Figs. 7 and 8).

d. Significance of the curl features

Summaries of standard errors of the curl estimates (e.g., Fig. 5) indicate that the mode of the distribution of standard errors will lie near 1×10^{-8} dyn cm^{-3} (i.e., one contour interval in Figs. 7–10) for data densities of the order of 200–300 observations per one-degree square. For one contour interval to generally correspond to about two standard error units, it would require on the order of 1000 observations per one-degree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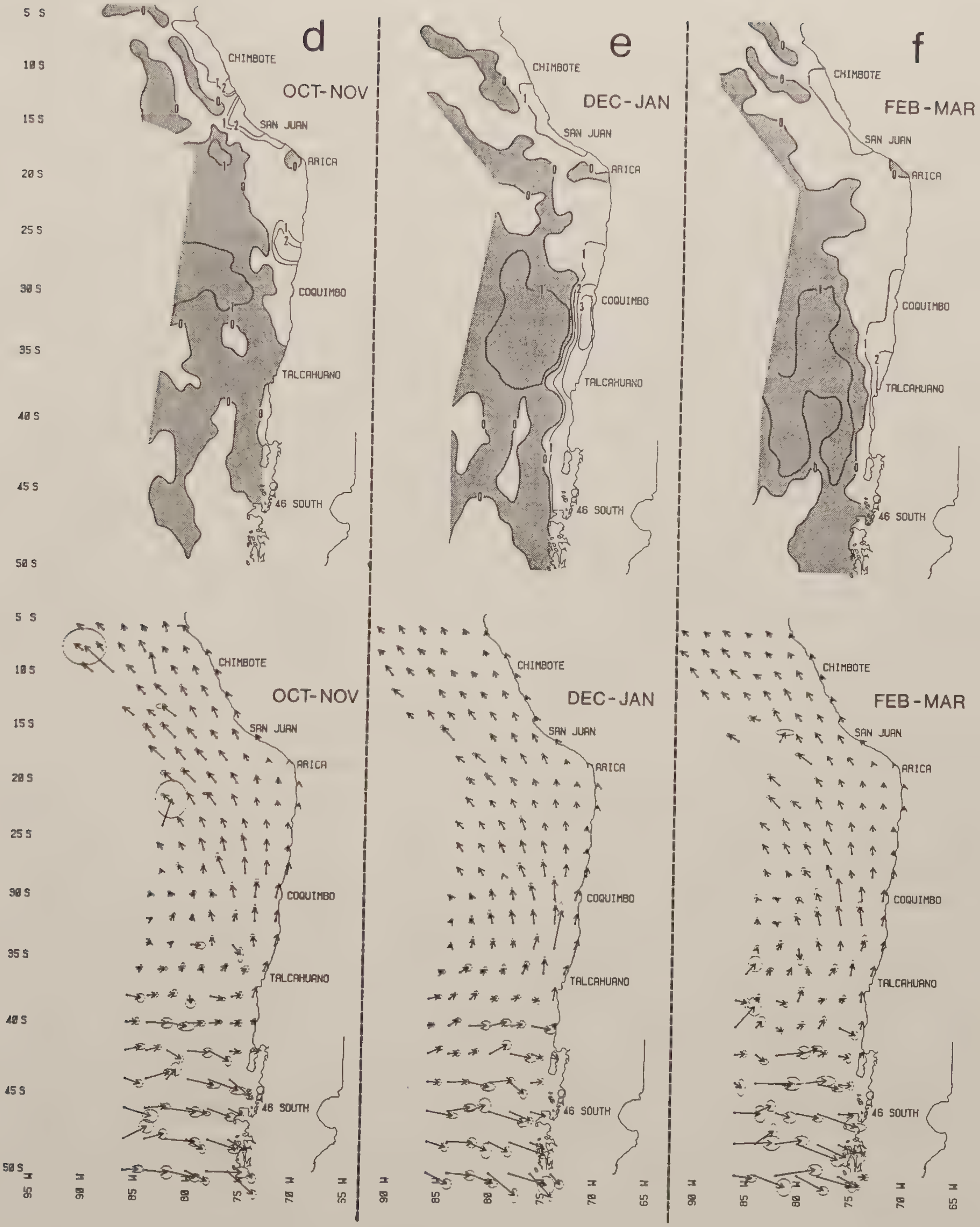
dyne cm^{-2}

FIG. 10. Peru/Humboldt Current region: wind-stress curl (10^{-8} dyn cm^{-3}) and surface wind-stress (dyn cm^{-2}) distributions. Contour interval is 1×10^{-8} dyn cm^{-3} and regions of anticyclonic curl are shaded. Wind-stress vectors are plotted at alternate latitude and longitude intersections, and symbols are scaled according to the key on the chart. (a) April–May, (b) June–July, (c) August–September,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15 S
20 S
25 S
30 S
35 S
40 S
45 S
50 S
95 W
90 W
85 W
80 W
75 W
70 W
65 W

FIG. 10. (*Continued*) (d) October–November, (e) December–January, and (f) February–March.

square. In the process used to construct the fields, a large proportion of highly significant estimates allows quite a fine scale of detail (~1° to 2° scale) to be reinserted into the smoothed distributions, even after the discard of estimates either carrying large standard errors or lacking consistency between adjacent one-month subsamples.

Reference to Fig. 3 indicates high frequencies of significant curl estimates on the 1° scale might be expected in areas roughly corresponding to shaded areas of Figs. 3a, 3b, and 3d. (Recall that the data densities shown in Fig. 3 should be reduced by a factor of approximately $1/12$ to reflect the density of data actually used in the curl estimates for each 2-month seasonal segment in those three regions.)

For example, the curl features shown off the Iberian Peninsula (Fig. 8) during spring and summer are judged to be highly significant on small scales (approaching 1°), both because of the extremely high data densities in that region and because multiple contours define rather small-scale features. Likewise, intense curl features near the coast along northwest Africa, south of Cabo Bojador, are likewise expected to be highly significant. However, those features to the north of Cabo Bojador are more questionable, particularly near the coast. In the California Current region (Fig. 7), the intense wind-stress curl indicated for the Southern California Bight likewise appears to be highly significant on small scales. Along the coast of Baja California one also finds adequate numbers of observations, but few features are strongly defined (i.e., by more than a single contour interval).

In other regions with lower data densities, our distributions lack significant features on such small scales. This results because the lack of highly stable features (i.e., carrying small standard errors in the 1° estimates and consistency among independent 1-month subsamples) has prevented small-scale details from being reinserted into the objectively smoothed distributions by the subjective analysis process. In some extremely data-poor regions offshore of Chile there are large areas where the characteristic one-degree sample size is only on the order of 10 to 20 observations per 1° square per 2-month seasonal segment. In these cases, the filtered distributions were too noisy to be effectively contoured, even on the 3° × 3° scale, and contours had to be drawn very roughly through large areas of ocean (in some cases on the 5° to 10° scale). Obviously, detailed locations of single contours that are not associated with nearby contours (i.e., that reflect less than one contour interval of gradient) are not to be taken very seriously in any of the areas and certainly not in data-poor regions, such as off western South America.

In attempting to merge information that may be significant on different scales in different parts of the distributions into a single description, we recognize certain problems in conveniently judging significance. The only scales that are consistently supported by sufficient data in all of the areas treated are the rather large (~10°) scales for which descriptions have already been made available (e.g., Hellerman and Rosenstein 1983). However, real, significant features supported by real data on much smaller scales exist that undoubtedly have important dynamical and ecological consequences in these eastern boundary current regions. We have done our best to "squeeze out" the smallest data-supported scales at every location while being conservative. Our purpose has been to avoid depicting features of quite questionable validity. Therefore, a lack of fine-scale wind-stress curl features in certain parts of the distributions does not mean that no such detail exists, but that we cannot confidently assert that it does.

We believe that the easiest and most useful gauge of significance of the features shown in Figs. 7–10 is the consistency exhibited among the independent distributions for different 2-month segments of the annual cycle. As described above, care has been taken to avoid transferring any information between such segments (i.e., we have consciously avoided interpretive contouring of the data in light of previously contoured distributions for the same area). Thus, when a feature exhibits consistency or regular seasonal progression through a portion of the annual cycle (i.e., between independent adjacent 2-month segments), we suggest that the reader consider it as being a real characteristic feature of the actual long-term mean wind-stress curl field. When any feature appears in only one of the distributions, without reasonable corroboration in the adjacent 2-month seasonal segments, it should be ignored. Indeed, this is the point of view taken in the descriptions that follow.

3. Results

a. The California Current region

Anticyclonic wind-stress curl, associated with the generally equatorward wind flow within the eastern leg of the North Pacific subtropical anticyclone, dominates the offshore portions of the California Current region (Fig. 7). Adjacent to the coast, the wind-stress curl tends to be cyclonic. Thus, Ekman divergence dominates at the ocean surface near the coast, and Ekman convergence is dominant in the offshore region.

The transition zone between the regions of cyclonic and anticyclonic curl is associated with an offshore maximum in the alongshore wind stress. This contour of zero curl lies approximately 200 to 300 km offshore and parallels the coastline along the entire eastern boundary between northern Baja California and Vancouver Island, from April through September (Figs. 7d, 7e, and 7f). The cross-shore profile of alongshore stress shows a decrease in magnitude on either side of the maximum. This structure, which is very characteristic of these climatological distributions, was previously noted by Munk (1950), Yoshida and Mao

(1957), Reid et al. (1958), and Nelson (1977). Moreover, the strong tendency for the alongshore wind stress to increase with distance from the coast (and for the nearshore coastal upwelling regime to be influenced by cyclonic wind-stress curl) is also evident from more recent observational studies off the coasts of Oregon and central California, as described by Halpern (1976), Beardsley et al. (1987), and Huyer and Kosro (1987).

A local maximum of cyclonic curl is associated with the Southern California Bight throughout the year. During fall and winter (Figs. 7a and 7b) substantial cyclonic curl extends northward along the coast from the Southern California Bight, nearly reaching Cape Mendocino. In late winter and spring (Figs. 7c and 7d) a second local maximum extends south from Cape Mendocino to include the area off San Francisco and Monterey Bay. By early summer, when the seasonal coastal upwelling regime has extended northward to influence essentially the entire west coast of the United States (Bakun et al. 1974), strong cyclonic curl is the rule along nearly the entire coastline of the region (Fig. 7e). In late summer, the strongest wind-stress curl in the region tends to be located adjacent to Cape Mendocino (Fig. 7f).

Throughout the year there is a consistent tendency for a lobe of anticyclonic curl to penetrate coastward from the offshore region to contact the coast of Baja California in the vicinity of Punta Baja, separating cyclonic curl regions to the north and south. Punta Baja is the site of the local maximum in coastal upwelling (Bakun and Nelson 1977). In this area, maximum equatorward alongshore wind stress occurs at the coast. This particular anticyclonic curl feature is an exception to the general pattern noted elsewhere in the region (and also in the other regions shown in Figs. 8, 9, and 10) of cyclonic curl extending some hundreds of kilometers seaward of coastal upwelling regimes.

Diagonal hatching in the area off the coast of the Pacific Northwest, shown in Fig. 7, is inserted to indicate an apparent tendency for anticyclonic wind-stress curl to exist very near the coast. The unsmoothed monthly distributions in this region have a particularly noisy appearance, with indications of generally cyclonic curl being interrupted by intense bull's-eyes of anticyclonic curl, which are generally confined to a single grid point and are characterized by large standard errors. When the averaging period is expanded, these bull's-eyes tend to coalesce, so that in the composite annual mean the area directly adjacent to the coast is predominantly occupied by anticyclonic wind-stress curl. On the scale of these computations, the situation very near the coasts of Oregon and Washington appears to be a variable mixture of more persistent weak cyclonic curl (perhaps related to lateral boundary layer effects in situations where winds are directed equatorward), broken intermittently by more intense episodes of anticyclonic curl (perhaps related to poleward winds associated with storm events). Higher resolution (0.2° × 0.2° grid) distributions of wind stress (unpublished data) for this portion of the coast show certain indications of a characteristic maximum of equatorward wind stress within about 10 km of the coast.

One of the purposes of the present study was to check for suspected scale-related artifacts in Nelson's (1977) wind stress and wind-stress curl distributions, which have been widely used in diagnosing the dynamics of the California Current System. In general, the offshore scale of major wind-stress curl features exhibited in the smaller-scale "staggered grid" curl estimates (Fig. 7) is consistent with Nelson's earlier work. However, certain local instances of offshore "bowing" of curl contours seaward of coastal indentations seen in Nelson's maps are much attenuated in these revised distributions (Fig. 7). Apparently these bowed features are scale-related artifacts, where the strong curl due to "wind shadow" in the coastal indentations propagates seaward due to the scale of the computation. Thus, the staggered grid technique (Fig. 1b) appears to provide a substantial improvement over the more standard finite difference method near boundary features, where a quite abrupt small-scale pattern exists. One additional advantage of the staggered grid technique is that only directly adjacent curl estimates share data. This makes it easier to subjectively recognize, or to objectively filter, alternating intense spikes of positive and negative curl, which are indicative of "data problems" in the particular shared gridpoint sample (see section 2c).

b. The Canary Current region

North of about 15°N, the Canary Current region (Fig. 8) exhibits a similar general dominance of anticyclonic wind-stress curl offshore and cyclonic curl adjacent to the coast. This characteristic pattern conforms to Mittelstaedt's (1983) description of seasonal variations of winds and surface circulation off northwest Africa. Near 15°N, the anticyclonic curl tends to be truncated by a zonal band of cyclonic curl that extends seaward to beyond the area treated in this study. During fall (Fig. 8a) cyclonic curl maxima are located in coastal bights off Ifni and between Cap Blanc and Cap Vert. As the seasons progress, the maxima shift to positions more directly associated with major capes. Particularly strong cyclonic curl lies directly adjacent to Cap Sim during spring and summer (Figs. 8d and 8e), the seasons of vigorous coastal upwelling (Wooster et al. 1976). Near the coast of the Iberian Peninsula, the mean curl distribution is rather weak and irregular during fall and early winter, but becomes strongly cyclonic during spring and summer, when spatially separated wind-stress curl maxima appear adjacent to the northwestern coast of the Iberian Peninsula and off southern Portugal. Although cyclonic curl near the coastal boundary appears to be the general rule, McClain et al. (1980) observed strong anticyclonic curl adjacent to the coast at Cape Finisterre, Spain, which they related to channeling of winds along the axes of the rias (inlets), located on the northwest coast of Spain. Such features appear to be intermittent and narrowly confined to the coast and, therefore, cannot be resolved by these methods.

A lobe of anticyclonic wind-stress curl extends to the coast near Cabo Bojador during fall and winter (Figs. 8a, 8b, and 8c). The position of this lobe relative to the equatorward wind flow in the subtropical anticyclone is fairly similar to that of the persistent lobe of anticyclonic curl off Punta Baja in the California Current region. However, the lobe off Cabo Bojador and a similar lobe north of Cap Sim do not exhibit the same degree of persistence through the spring and summer upwelling seasons. In fact, the areas off Cap Sim and Cabo Bojador tend to be sites of strong cyclonic curl in the spring through late summer (Figs. 8d, 8e, and 8f). Moreover, a lobe of anticyclonic wind-stress curl, rather than being associated with any coastal protuberance, appears to extend directly into the coastal bight near Ifni during late spring and early summer.

An interesting tendency for the offshore area of anticyclonic curl to be split by a region of cyclonic (or very weak anticyclonic) curl in the region some 5° to 10° longitude offshore, from Cabo Bojador to somewhat south of Cap Blanc, appears in most of the Canary Current distributions. The area from about 10° to 20°N is characterized by cyclonic wind-stress curl during the summer months (Figs. 8e and 8f). However, during the other seasons of the year, a region of anticyclonic curl extends to the south of Cap Vert between 21° and 25°W.

c. The Benguela Current region

In the Benguela Current region, the coastal area of cyclonic wind-stress curl appears as a wedge extending from the vicinity of 20°S, narrowing in offshore extent toward the south. The wedge has its most limited poleward extent in austral winter (Fig. 9b) when it reaches to just south of Lüderitz. By early spring the wedge has extended to Cape Columbine (Fig. 9c) and beyond the Cape of Good Hope by late spring (Fig. 9d), where it remains until it retreats northward again with the approach of austral winter.

Equatorward of 20°S, the distributions are less distinct. A sparsity of observations in that region (Fig. 3d), and associated large sampling errors, make the computed curl distributions very noisy and somewhat uncertain. However, one very persistent feature is an area of anticyclonic curl, some hundreds of kilometers in diameter lying about 200 km offshore, and extending somewhat northward of Cape Frio. Evidence for this particular feature is found in all 12 independent monthly distributions. In the region north of 15°S, there appears to be some tendency for anticyclonic curl near the coast in late austral winter to spring. In austral summer and fall, the region within 700 km of the coast appears to be dominated by cyclonic wind-stress curl.

d. The Peru/Humboldt Current region

During austral fall (Fig. 10a) in the Peru/Humboldt Current region, cyclonic curl adjacent to the coast extends south to the vicinity of Talcahuano. Local curl maxima appear along the coast of Peru from the vicinity of San Juan to north of Chimbote, and off Chile at about 25°S. The maximum off Peru appears to maintain its location throughout the year, strengthening in austral winter and relaxing somewhat in summer. The wind-stress curl maximum off Chile moves poleward from winter to summer, reaching maximum intensity off the stretch of coastline from 30° to 34°S in austral summer (Fig. 10e). This maximum appears to move even farther south in late summer (Fig. 10f), to a position just north of Talcahuano, before weakening greatly and retreating back northward in fall.

There are consistent indications of anticyclonic curl within the coastal bight near Arica. This is in contrast to the consistent cyclonic curl found to characterize major coastal bights in other eastern boundary current regions, for example, in the Southern California Bight (Fig. 7) and between Cap Blanc and Cap Vert (Fig. 8). This is probably due to the fact that the coastal shape here is such that the equatorward wind, which flows along the Chilean coast, blows uninterruptedly into the bight, rather than being deflected by a major change in coastline orientation at the upwind edge of the bight.

A persistent, elongated lobe of anticyclonic curl exists off northern Peru. This feature is definitely separated from the general anticyclonic curl in the offshore region to the south. In view of the low data density available for the region, the consistency of this lobe in location and general shape among these independently prepared distributions is remarkable. The lobe appears to be aligned along the axis of the trade wind flow, which veers westward away from the coast in that area.

4. Generalizations

Eastern boundary current regions are characterized by anticyclonic wind-stress curl in the offshore portions. Near the coastal boundary, the wind-stress curl tends to be cyclonic, particularly during the coastal upwelling seasons (i.e., seasons in which the average wind stress is directed alongshore and equatorward). These cyclonic curl areas typically extend 200 to 300 km offshore. Thus, the coastal upwelling that occurs within several tens of kilometers of the coast is typically augmented by upward Ekman pumping (oceanic upwelling) over a much larger offshore extent. The coastal cyclonic curl regions tend to have their greatest alongshore extents during the summer seasons in the respective hemispheres.

Particularly intense cyclonic wind-stress curl is found adjacent to capes during summer coastal upwelling maxima. During seasons of strong equatorward, alongshore wind stress, the offshore profile of stress bears at least a qualitative resemblance to a lateral frictional boundary layer, characterized by an offshore maximum in wind velocity and a decay of velocity toward the coast. Coastal protuberances would tend to narrow the layer locally, leading to intensified cyclonic curl.

The alongshore jet structure of the low-level winds off the western United States has been modeled by Chao (1985) as a boundary layer response of the large-scale zonal westerlies to blocking by the coastal mountain ranges along the west coast of North America. Chao also indicates that thermal forcing by the land–ocean temperature contrast could reinforce the jet structure during the summer and, thereby, account for the observed intensification of alongshore wind near the coast during the summer season.

During fall and winter when the upwelling system weakens, the most intense cyclonic curl is associated with coastal bights. During winter, the regime tends to be intermittently broken by the passage of cyclonic storms, which often involve intense winds having poleward and onshore components. Although maritime data cannot define synoptic situations on these small spatial scales, it would seem reasonable that such winds might tend to reach maximum velocities as they are narrowed and deflected toward a more alongshore direction, directly adjacent to the barrier presented by the coastal boundary. Such effects might tend to be strongest where the wind flow was directed into coastal bights, leading to the tendency during winter for cyclonic curl maxima to lie within such concave coastal segments.

In various locations, such as at Punta Baja in the California Current region, near Cabo Bojador and Cap Sim in the Canary Current region, slightly to the north and offshore of Cape Frio in the Benguela Current region, and offshore of Chimbote in the Peru/Humboldt region, distinctive lobes, or isolated patches of anticyclonic curl, appear either in contact with, or within several hundred kilometers of, the coastal boundary. These appear typically to be located in areas where the equatorward wind flow begins to veer offshore to merge into the tropical trade-wind circulation.

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REFERENCES

Abbott, M. R., and P. M. Zion, 1987: Spatial and temporal variability of phytoplankton pigment off northern California during Coastal Ocean Dynamics Experiment 1. *J. Geophys. Res.*, **92**, 1745–1755.

Bakun, A., 1978: Guinea Current upwelling. *Nature*, **271**, 147–150.

——, 1990: Global climate change and intensification of coastal ocean upwelling. *Science*, **247**, 198–201.

——, and C. S. Nelson, 1977: Climatology of upwelling related processes off Baja California. California Cooperative Oceanic Fisheries Investigations Reports, 19, 107–127.

——, and R. H. Parrish, 1990: Comparative studies of coastal pelagic fish reproductive habitats: The Brazilian sardine (*Sardinella aurita*). *J. Cons. Int. Explor. Mer.*, **46**, 269–283.

——, D. R. McLain and F. V. Mayo, 1974: The mean annual cycle of coastal upwelling off western North America as observed from surface measurements. *Fish. Bull.*, **72**, 843–844.

Beardsley, R. C., C. E. Dorman, C. A. Friehe, L. K. Rosenfeld and C. D. Winant, 1987: Local atmospheric forcing during the Coastal Ocean Dynamics Experiment, 1. A description of the marine boundary layer and atmospheric conditions over a northern California upwelling region. *J. Geophys. Res.*, **92**, 1467–1488.

Beaton, A. E., and J. W. Tukey, 1974: The fitting of power series, meaning polynomials, illustrated on band-spectroscopic data. *Technometrics*, **16**, 147–185.

Beers, Y., 1953: *Introduction to the Theory of Error.* Addison-Wesley, 65 pp.

Blanc, T. V., 1985: Variation of bulk-derived surface flux, stability, and roughness results due to the use of different transfer coefficient schemes. *J. Phys. Oceanogr.*, **15**, 650–669.

Böning, C. W., R. Döscher and H.-J. Isemer, 1991: Monthly mean wind stress and Sverdrup transports in the North Atlantic: A comparison of the Hellerman-Rosenstein and Isemer-Hasse climatologies. *J. Phys. Oceanogr.*, **21**, 221–235.

Breidenbach, J., 1990: EOFs of pseudostress over the Indian Ocean (1977–85). *Bull. Amer. Meteor. Soc.*, **71**, 1448–1454.

Brink, K. H., D. C. Chapman and G. R. Halliwell, Jr., 1987: A stochastic model for wind-driven currents over the continental shelf. *J. Geophys. Res.*, **92**, 1783–1797.

Cardone, V. J., J. G. Greenwood and M. A. Cane, 1990: On trends in historical marine wind data. *J. Climate*, **3**, 113–127.

Carton, J. A., and S. G. H. Philander, 1984: Coastal upwelling viewed as a stochastic phenomenon. *J. Phys. Oceanogr.*, **14**, 1499–1509.

Chao, S.-Y., 1985: Coastal jets in the lower atmosphere. *J. Phys. Oceanogr.*, **15**, 361–371.

Chelton, D. B., 1980: Low frequency sea level variability along the west coast of North America. Ph.D. dissertation, University of California, San Diego, 212 pp.

——, 1982: Large-scale response of the California Current to forcing by the wind-stress curl. California Cooperative Oceanic Fisheries Investigations Reports, 23, 130–148.

Cleveland, W. S., 1981: LOWESS: A program for smoothing scatterplots by robust locally weighted regression. *Amer. Statist.*, **35**, p. 54.

Cummins, P. F., L. A. Mysak and K. Hamilton, 1986: Generation of annual Rossby waves in the North Pacific by the wind-stress curl. *J. Phys. Oceanogr.*, **16**, 1179–1189.

Düing, W., F. Ostapoff and J. Merle, 1980: *Physical Oceanography of the Tropical Atlantic during GATE.* University of Miami, 117 pp.

Evenson, A. J., and G. Veronis, 1975: Continuous representation of wind stress and wind-stress curl over the world ocean. *J. Mar. Res.*, **33**(Suppl.), 131–144.

Goldenberg, S. B., and J. J. O'Brien, 1981: Time and space variability of tropical Pacific wind stress. *Mon. Wea. Rev.*, **109**, 1190–1207.

Halpern, D., 1976: Measurements of near-surface wind stress over an upwelling region near the Oregon coast. *J. Phys. Oceanogr.*, **6**, 108–112.

Hastenrath, S., and P. J. Lamb, 1977: *Climatic Atlas of the Tropical Atlantic and Eastern Pacific Oceans.* University of Wisconsin Press, 15 pp., 97 figs.

Hellerman, S., and M. Rosenstein, 1983: Normal monthly wind stress over the world ocean with error estimates. *J. Phys. Oceanogr.*, **13**, 1093–1104.

Hickey, B. M., 1979: The California Current System—hypotheses and facts. *Progress in Oceanography,* Vol. 8, Pergamon, 191–279.

Hsiung, J. 1986: Mean surface energy fluxes over the global ocean. *J. Geophys. Res.*, **91**, 10 585–10 606.

Hurlburt, H. E., and J. D. Thompson, 1973: Coastal upwelling on a β-plane. *J. Phys. Oceanogr.*, **3**, 16–32.

Huyer, A., and P. M. Kosro, 1987: Mesoscale surveys over the shelf and slope in the upwelling region near Point Arena, California. *J. Geophys. Res.*, **92**, 1655–1681.

Isemer, H.-J., and L. Hasse, 1991: The scientific Beaufort equivalent scale: Effects on wind statistics and climatological air–sea flux estimates in the North Atlantic Ocean. *J. Climate,* **4**, 819–836.

Large, W. G., and S. Pond, 1981: Open ocean momentum flux measurements over the ocean. *J. Phys. Oceanogr.*, **11**, 324–336.

McClain, C. R., S.-Y. Chao, L. P. Atkinson, J. O. Blanton and F. de Castillejo, 1986: Wind-driven upwelling in the vicinity of Cape Finisterre, Spain. *J. Geophys. Res.*, **91**, 8470–8486.

McCreary, J. P., Jr., P. K. Kundu and S.-Y. Chao, 1987: On the dynamics of the California Current system. *J. Mar. Res.*, **45**, 1–32.

Mittelstaedt, E., 1983: The upwelling area off northwest Africa—a description of phenomena related to coastal upwelling. *Progress in Oceanography,* Vol. 12, Pergamon, 307–331.

Munk, W. H., 1950: On the wind-driven ocean circulation. *J. Meteor.*, **7**, 79–93.

Nelson, C. S., 1977: Wind stress and wind-stress curl over the California Current. NOAA Tech. Rep. NMFS SSRF-714, U.S. Dept. of Commerce, 87 pp.

Parrish, R. H., A. Bakun, D. M. Husby and C. S. Nelson, 1983: Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish reproduction. *Proc. of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources,* G. D. Sharp and J. Csirke, Eds., *FAO Fish. Rep.*, San Jose, Costa Rica, FAO, 291, 731–778.

Pedlosky, J., 1974: Longshore currents, upwelling, and bottom topography. *J. Phys. Oceanogr.*, **4**, 214–226.

Peláez, J., and J. A. McGowan, 1986: Phytoplankton pigment patterns in the California Current as determined by satellite. *Limnol. Oceanogr.*, **31**, 927–950.

Perigaud, C., P. Delecluse and J. F. Minster, 1989: Wind stress over the Arabian Sea from ship reports and Seasat scatterometer data. *Mon. Wea. Rev.*, **117**, 2348–2364.

Rabiner, L. R., M. R. Sambur and C. E. Schmidt, 1975: Applications of a nonlinear smoothing algorithm to speech processing. *IEEE Trans. Acoust., Speech Signal Proc.*, **ASSP-23**, 552–557.

Ramage, C. S., 1987: Secular change in reported surface wind speeds over the oceans. *J. Climate Appl. Meteor.*, **26**, 525–528.

Reid, J. L., Jr., G. I. Roden and J. G. Wyllie, 1958: Studies of the California Current system. California Cooperative Oceanic Fisheries Investigations Reports, **6**, 28–56.

Rienecker, M. M., and L. L. Ehret, 1988: Wind-stress curl variability over the North Pacific from the Comprehensive Ocean–Atmosphere Data Set. *J. Geophys. Res.*, **93**, 5069–5077.

——, C. N. K. Mooers and A. R. Robinson, 1987: Dynamical interpolation and forecast of the evolution of mesoscale features off northern California. *J. Phys. Oceanogr.*, **17**, 1189–1213.

Roden, G. I., 1972: Large-scale upwelling off northwestern Mexico. *J. Phys. Oceanogr.*, **2**, 184–189.

Saunders, P. M., 1976: On the uncertainty of wind-stress curl calculations. *J. Mar. Res.*, **34**, 155–160.

Servain, J., and D. M. Legler, 1986: Empirical orthogonal function analysis of tropical Atlantic sea surface temperature and wind stress. *J. Geophys. Res.*, **91**, 14 181–14 191.

Shearman, R. J., 1983: The Meteorological Office main data bank. *Meteor. Mag.*, **112**, 1–10.

Smith, R. L., 1968: Upwelling. *Oceanogr. Mar. Biol. Ann. Rev.*, **6**, 11–46.

Smith, S. D., 1988: Coefficients for sea surface wind stress, heat flux, and wind profiles as a function of wind speed and temperature. *J. Geophys. Res.*, **93**, 15 467–15 472.

Trenberth, K. E., W. G. Large and J. G. Olson, 1989: The effective drag coefficient for evaluating wind stress over the oceans. *J. Climate,* **2**, 1507–1516.

Weare, B. C., 1989: Uncertainties in estimates of surface heat fluxes derived from marine reports over the tropical and subtropical oceans. *Tellus,* **41A**, 357–370.

White, W. B., 1985: The resonant response of interannual baroclinic Rossby waves to wind forcing in the eastern midlatitude North Pacific. *J. Phys. Oceanogr.*, **15**, 403–415.

Willebrand, J., 1978: Temporal and spatial scales of the wind field over the North Pacific and North Atlantic. *J. Phys. Oceanogr.*, **8**, 1080–1094.

Wooster, W. S., and J. L. Reid, Jr., 1963: Eastern boundary currents. *The Sea,* Vol. 2, M. N. Hill, Ed., Wiley Interscience, 253–280.

——, A. Bakun and D. R. McLain, 1976: The seasonal upwelling cycle along the eastern boundary of the North Atlantic. *J. Mar. Res.*, **34**, 131–141.

Wyrtki, K., and G. Meyers, 1976: The trade wind field over the Pacific Ocean. *J. Appl. Meteor.*, **15**, 698–704.

Yoshida, K., 1955a: Coastal upwelling off the California coast. *Rec. Oceanogr. Works Japan,* **2**, 8–20.

——, 1955b: An example of variations in oceanic circulation in response to the variations in wind field. *J. Oceanogr. Soc. Japan.*, **11**, 103–108.

——, and H.-L. Mao, 1957: A theory of upwelling of large horizontal extent. *J. Mar. Res.*, **16**, 40–54.

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Comparative studies of coastal pelagic fish reproductive habitats: the anchovy (*Engraulis anchoita*) of the southwestern Atlantic

Andrew Bakun and Richard H. Parrish

Bakun, A., and Parrish, R. H. 1991. Comparative studies of coastal pelagic fish reproductive habitats: the anchovy (*Engraulis anchoita*) of the southwestern Atlantic. – ICES J. mar. Sci., 48: 343–361.

A framework of comparative climatology of reproductive habitats of coastal pelagic fishes is extended to the anchovy inhabiting the shelf-sea ecosystem off Argentina, Uruguay, and southern Brazil. Maritime weather reports are summarized to yield distributions of wind stress, cloud cover, insolation, sea-surface temperature, wind mixing index, and Ekman transport. These distributions are considered together with other known aspects of the oceanography of the region and with seasonal and geographical aspects of reproductive activity. Over its extensive range, *Engraulis anchoita* spawns successfully within three different configurations of environmental processes affecting transport, water column stability, and trophic enrichment. One of these, incorporating a coastal indentation downstream from a coastal upwelling center, is very similar to the most common configuration characterizing spawning grounds of eastern ocean anchovy populations. The second, featuring interleaving water masses and upwelling at the continental shelf break, exhibits similarities to the reproductive habitat of the South African anchovy. The third, involving tidal mixing fronts, has been previously noted primarily in connection with herring of higher-latitude, shallow shelf-sea systems. The study adds support to the idea that similar fish populations in different regions must solve similar basic environmental problems and that various experiences of environmental effects in different populations, when viewed from a properly posed conceptual framework, can add up to a useful accumulation of insight.

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Introduction

The population of *Engraulis anchoita*, a representative temperate zone anchovy species, extends along the Atlantic coast of South America from southern Brazil to southern Argentina. No biomass estimates are available for the entire population; however, according to Sánchez (1989) the biomass in the region off Argentina varied between 4.0 and 6.2 million metric tonnes in eight surveys made during 1967–1983. *Engraulis anchoita* is presently lightly exploited, with about 25 000 t being taken annually. It is an extremely important component of the regional ecosystem, being a major food source for a variety of predators. Hake (*Merluccius* spp.) alone, for example, may consume one million tonnes per year.[1]

Anchovies of the genus *Engraulis* comprise an extremely important component of the fishery production of the world. The Peruvian anchoveta (*Engraulis ringens*) prior to its collapse was by far the largest single fishery stock on record, reaching a peak annual production of 12 million tonnes in 1970 and by itself accounting for some one-sixth of the world's total fishery production over the period 1963–1972. Landings of the European anchovy (*Engraulis encrasicolus*) have reached 0.8 million tonnes (1984). The population of South African anchovy (*Engraulis capensis*) supported rather stable catches of 0.2 to 0.3 million tonnes for a number of years; recently the catches have increased dramatically to approach a million tonnes in 1987 (FAO, 1990). Annual catches of northern anchovy (*Engraulis mordax*) in the northeastern Pacific Ocean off the western USA and northern Mexico have been as high as 0.4 million tonnes (1981). In the northwestern Pacific, annual catches of Japanese anchovy (*Engraulis japonica*) have recently declined somewhat from a 1965 level of nearly 0.5 million tonnes. Clupeoid fishes such as anchovies and sardines are relatively short-lived, highly productive organisms which feed low in the trophic pyramid, often directly on phytoplankton. As well as being commercially important in themselves, they constitute an extremely important food base for other valuable fish species.

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[1] Lasta, C. (Verbal presentation) IOC-FAO Sardine/Anchovy Recruitment Project (SARP) Consultation, La Jolla, California, 5–9 November, 1984.

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In this paper, we examine the habitat climatology of *Engraulis anchoita* (which we call by its local name "anchoita"). The purpose is to continue to build a basis for application of the comparative method (Mayr, 1982) to the problem of identifying the physical–biological linkages controlling the population dynamics of coastal pelagic fishes. The primary environmental data source, the archived files of surface marine weather reports, is the same as used in our previous studies (e.g. Parrish *et al.*, 1981; Bakun and Parrish, 1982; Parrish *et al.*, 1983; Bakun, 1985; Bakun and Parrish, 1990). These data are available at varying densities for all regions of the oceans of the world. Thus, they represent an opportune resource for incorporating a great variety of species, habitats, and regions within a global comparative context.

In previous studies of seasonality and geography of anchovy and sardine spawning activity in eastern ocean upwelling ecosystems (Parrish *et al.*, 1981; Bakun and Parrish, 1982; Parrish *et al.*, 1983; Bakun, 1985; Roy *et al.*, 1989), a general pattern has begun to emerge. In addition to the trophic enrichment associated with the upwelling process, seasons and/or locations promoting retention of larvae near the coast while minimizing turbulent mixing of the water column appear to be favored. Temperature itself, while setting limits on geographical extents of species distributions, appears to be less important in defining favorable spawning conditions within these limits. Observational and experimental foundation for this view has been provided by the distinguished work of Reuben Lasker and his co-workers at the NOAA-NMFS Southwest Fisheries Science Center (e.g. Lasker, 1975, 1978, 1988). Several recent time series modeling studies (Mendelssohn and Mendo, 1987; Peterman and Bradford, 1987; Cury and Roy, 1989), addressing inter-year variability in reproductive success, have tended to confirm the pattern.

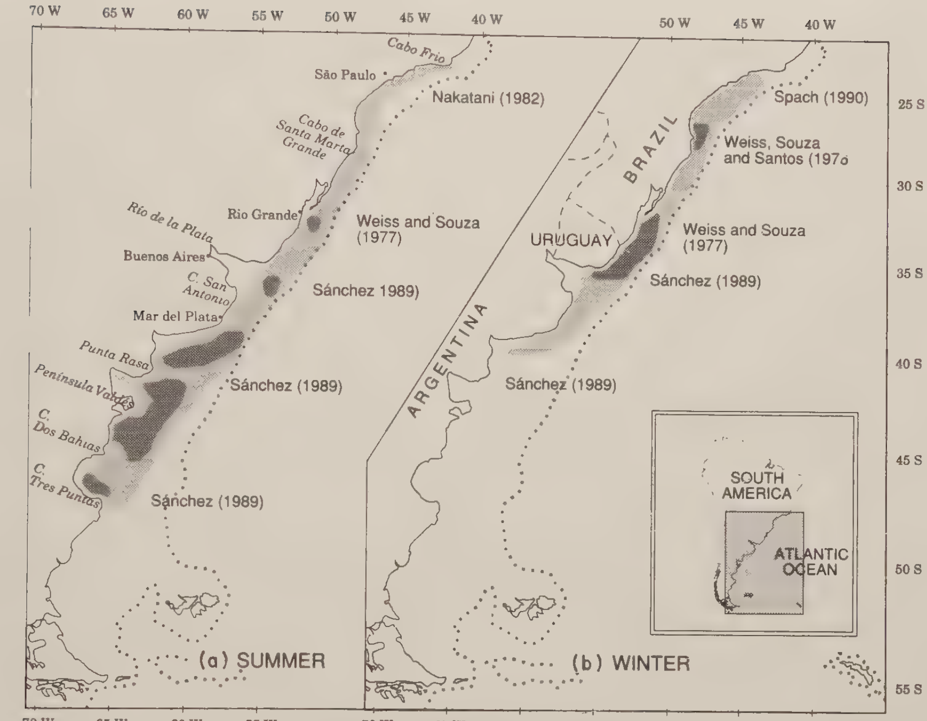
Western ocean boundary regions are dynamically quite different from the regions along eastern ocean boundaries. For example, there are particularly strong influences of advected momentum and generally more intense horizontal gradients in temperature and other properties. However, Bakun and Parrish (1990) found a nearly identical configuration of mechanisms, although operating over a different temperature range, appearing to determine favorable reproductive habitat for both the Brazilian sardine (*Sardinella braziliensis* = *Sardinella aurita*) population spawning in a tropical western ocean boundary ecosystem off Southeastern Brazil and the Pacific sardine (*Sardinops sagax*) population spawning in a temperate eastern ocean boundary ecosystem off Southern California. This supports the idea that populations of small coastal pelagic fishes, whatever the specifics of their environmental setting, have generally similar basic requirements that must be met for them to gain a dominant position within the regional trophic pyramid.

The Brazilian sardine can be viewed as being primarily associated with a wind-driven coastal upwelling system, which is similar in many ways to coastal upwelling systems located along eastern ocean boundaries. In contrast, the bulk of the anchoita habitat is not influenced substantially by coastal upwelling; in fact, the opposite situation of onshore surface drift and resulting coastal downwelling is dominant. In this paper, we investigate the proposition that the basic requirements for a favorable reproductive habitat may nonetheless be very similar to those in upwelling regions, and in addition may be met in a rearranged configuration of the same set of dominant environmental processes. If so, the anchoita might be justifiably incorporated in a common comparative "framework", with respect to environmental dependencies, with many of the other major pelagic-spawning clupeoid fish populations of the world's coastal marine ecosystems.

In our opinion, the case for attempting to assemble such a framework is substantial. The "fishery-environment" problems appears to be one of moderate complexity, at the least. Some framework, even a hypothetical one, is needed to organize and array whatever events and experiences of fishery-environmental interactions may be available so that, rather than remaining a collection of isolated facts and anecdotes, they can support a useful accumulation of insight. Our approach in this is diagnostic, and we do not intend to imply rigorous hypothesis testing in pointing out the patterns of correspondence that we find. However, we hope that indicating mechanistically reasonable and pervasive patterns of association among important ecological processes might support the emergence of intellectually attractive, well-focused (but not fatally oversimplified) hypotheses that could motivate the kind of observational programs, survey designs, etc., that could support rigorous tests. One should note that hypotheses formulated in this manner, being diagnosed from characteristic seasonal and geographical adaptations and behaviors rather than depending in any way on time-series results, may be regarded as *a priori* hypotheses with respect to time-series analysis. That is, they may be a guide to the selection of variables for empirical tests in a way that does not deplete, by the selection process, the minimal degrees of freedom contained in available inter-year data series (Bakun, 1985).

Anchoita reproductive habitat climatology

Adult *E. anchoita* are abundant over an extensive region (22°–47°S), from north of Cabo Frio, Brazil (Matsuura *et al.*, 1985) to just north of Cabo Tres Puntas (Ciechomski and Sánchez, 1986). Eggs and larvae occur mainly over the continental shelf which is quite broad over much of the region, and they occur, at some time of the year, over essentially the same range of latitude as do the adults. The


70 W
65 W
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Cabo Frio
São Paulo
Nakatani (1982)
Cabo de Santa Marta Grande
Río de la Plata
Rio Grande
Weiss and Souza (1977)
Buenos Aires
C. San Antonio
Sánchez 1989)
Mar del Plata
Punta Rasa
Península Valdés
Sánchez (1989)
C. Dos Bahías
C. Tres Puntas
Sánchez (1989)
(a) SUMMER
BRAZIL
URUGUAY
ARGENTINA
Spach (1990)
Weiss, Souza and Santos (1976
Weiss and Souza (1977)
Sánchez (1989)
Sánchez (1989)
SOUTH AMERICA
ATLANTIC OCEAN
(b) WINTER
25 S
30 S
35 S
40 S
45 S
50 S
55 S

Figure 1. Coastwise extent of anchoita spawning. Light shading indicates range over which incidence of anchoita eggs has been observed. Darker shading indicates reports of substantial concentrations of eggs. (*Note that information is limited, particularly in the northern areas, and that therefore areas showing absence of concentrations may be questionable.*) References for the various features depicted are printed to the right of the areas to which they apply. The dotted line indicates the continental shelf limit (200 m isobath). (a) austral summer; (b) austral winter.

available information on the seasonal distribution of anchoita spawning has recently been reviewed (Castello, 1989; Mantero, 1989; Sánchez, 1989). Information is available for both seasonal and geographical distribution of spawning for the region off Argentina, where a large number of extensive egg and larvae surveys have been carried out. Information for the region off Uruguay and Brazil is based on a more limited number of surveys; data for the austral fall and winter are particularly sparse in the region between Cabo Frio (22°S) and Cabo de Santa Marta Grande (29°S), and no data are available for the austral summer for most of the region between Cabo de Santa Marta Grande (29°S) and Uruguay (34°S). Conclusions concerning the relative amount of spawning in the region between 22°S and 31°S must be considered preliminary as no part of the region has been surveyed twice in any of the four seasons.

During austral winter, the geographical distribution of spawning is at a minimum (Fig. 1); however, eggs and larvae are abundant off Brazil as far north as 23°S (Spach, 1990), considerable spawning occurs between 26° and 34°S (Weiss *et al.*, 1976; Weiss and Feijo de Souza, 1977), and eggs and larvae occur as far south as 40°S (Sánchez, 1989).

In spring, eggs and larvae are abundant as far north at 23°S (Nakatani, 1982; Hubold, 1982; G. Weiss, unpublished data),[2] they are at peak concentrations from 29°S to 41°S (Hubold, 1982; Sánchez, 1989; G. Weiss, unpublished data),[2] and spawning extends to about 44°S (Sánchez, 1989). Analysis of the reproductive cycle of the adults also demonstrates that reproduction peaks during the spring in northern Argentina (Brodsky and Cousseau, 1979).

The geographical extent of spawning is at a maximum during summer (Fig. 1). While still at significant levels in the region from Cabo Frio, Brazil (23°S) to Mar del Plata, Argentina (40°S), summer egg and larval concentrations are reduced from those which occur in the spring (Campaner and Honda, 1987; Weiss and Feijo de Souza, 1977; Sánchez, 1989). Eggs and larvae are at maximum concentrations between 41°S and 47°S during the summer (Sánchez, 1989).

Spawning is greatly reduced during the fall; however, eggs and larvae occur near the shelf break off São Paulo (23–27°S) in May (Nakatani, 1982; Campaner and Honda, 1987), in the vicinity of Rio Grande (29–34°S) in April (Hubold, 1982; G. Weiss, unpublished data),[2] and at relatively high concentrations off Uruguay and northern Argentina (34–38°S) throughout the fall (Sánchez, 1989).

In producing the seasonal distributions of environmental processes (Figs 2–5, 7) displayed in this section, we use the methods and procedures established in the companion paper (Bakun and Parrish, 1990; hereafter referred to as BP). Briefly, quantities of interest are estimated from individual maritime reports contained in the US National Climatic Center's file of marine surface observations (Tape Data Family – 11) and averaged by one-degree latitude/longitude quadrangles and by two-month segments of the calendar year. The vector quantities, wind stress, and Ekman transport were averaged by component (vector averaged). For reference to the formulations of the various types of estimates, and to the procedures followed in editing, smoothing of undersampled distributions, contouring, etc., we have included an adaptation of the "Methods" section from BP as an "Appendix" section to this paper.

The northern boundary of the mapped data displays (Figs 2–5, 7) overlaps the displays presented by BP. For the present study of the anchoita, there is no real need to extend the displays south of Cabo Tres Puntas (~47°S). However, the region further to the south is characterized by a very wide continental shelf and very important fishery resources, including hake, squid, pollock, etc. Because the distributions may be useful to other workers and studies, we have included the entire region as far south as the southeastern extremity of the South American Continent (Cabo San Diego) in the displays, even though the area south of 47°S latitude is not treated in the discussions of anchoita. Also, from time to time it will be useful to extend discussion northward beyond the northern limit of the data displays presented herein. In those instances, we will refer to the corresponding adjacent displays presented by BP.

Wind stress

The region lies largely within the latitude band of global-scale westerly winds. During the winter (Fig. 2a), the offshore area (i.e. the portion of the region more than about 500 km offshore) is marked by very strong westerly (eastward) stress exerted by the wind on the sea surface. A high degree of variability is indicated by the rather chaotic patterns of the vector symbols, which represent unsmoothed independent summaries of the available reports by one-degree latitude/longitude areal segments (thus differences between adjacent vector symbols in these distributions should not be regarded as meaningful small-scale detail, but rather as "sampling noise" due to data sparsity and consequent undersampling of a highly variable process). Also apparent at distances of several hundred kilometers from the coast is a tendency for anticlockwise veering and shearing of the vector field, implying predominance of anticyclonic wind stress curl in an offshore band parallel to the coastline trend.

With respect to this large-scale zonal flow, the area near the coast tends to lie in the "wind shadow" of the South American Continent. However, except to the north of Cabo San Antonio (~34°S), it remains a substantial fraction of one dyne cm^{-2} (0.1 Pa) during the winter season, even at near-coastal locations.

During summer (Fig. 2b), the magnitude of the wind stress is reduced substantially. The region of strong coherent westerly stress in the offshore region, which extended north of 30°S latitude in the winter, has receded south of 35°S. A region of particularly strong stress during the summer lies to the west and northwest of the Falkland (Malvinas) Islands; evidence of this feature is corroborated in the independently derived distributions for other two-month seasonal segments (not displayed for wind stress in this paper but displayed for the related turbulent mixing index and Ekman transport distributions in Figures 5 and 7). Very low average wind stress near the coast extends southward all the way to the vicinity of Cabo Dos Bahias (~45°S) during the summer.

Solar radiation and cloud cover

During the austral winter, the average portion of sky obscured by cloud cover (Fig. 3a) varies from about 50% to 55% in the extreme northern portion of the region to about 75% in the vicinity of the Falkand (Malvinas) Islands. Several local submaxima and subminima in cloud cover punctuate the larger scale north–south regional trend. For example, a strong local maximum corresponds to a region of particularly intense winds (Fig. 2a) near the seaward edge of the gridded area from ~40°S to ~46°S latitude.

The distribution of solar radiation penetrating the sea surface during winter (Fig. 3b) shows little effect of the details of the cloud cover pattern, being predominantly controlled by the very strong latitudinal gradient in day length and solar altitude which exists during the winter season. The effect of cloud cover is seen in minor features such as the northward bowing of the 20 watt m^{-2} isopleth over the Falklands.

During the summer, the cloud cover (Fig. 3c) is ~55% in the extreme northern portion of the region and ~70% near 55°S latitude. There is a general pattern of increased cloud cover near the offshore edge of the gridded area and

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[2] Weiss, G., Fundaçao Universidade do Rio Grande, Rio Grande, Brazil.

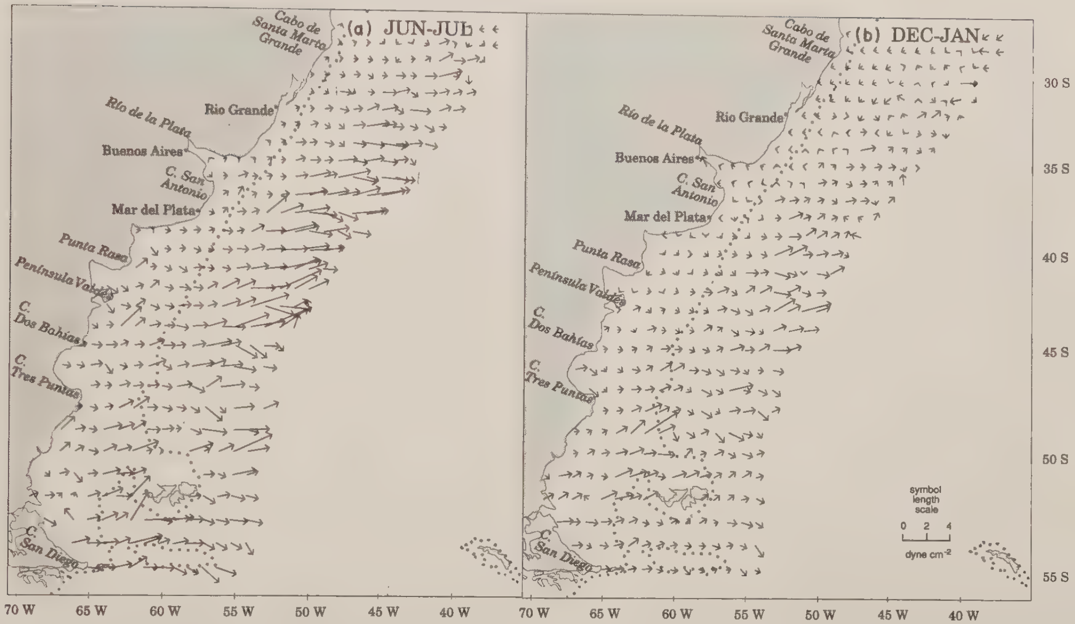


Figure 2. Sea surface wind stress distributions for (a) austral winter (June–July), and (b) austral summer (December–January). A symbol length scale is shown in panel (b). The dotted line indicates the continental shelf limit (200 m isobath).

a local maximum of average cloud cover (>70%) situated just north of the Falklands. The entire near-coastal region from Rio Grande (~32°S) to Península Valdéz (~43°S) appears as an area of rather minimal cloud cover during summer, with two large areas of less than 45% average cloud cover being separated by a band of slightly more than 45% which extends northeastward from the offshore region to intersect the coast near Mar del Plata (~35°–38°S).

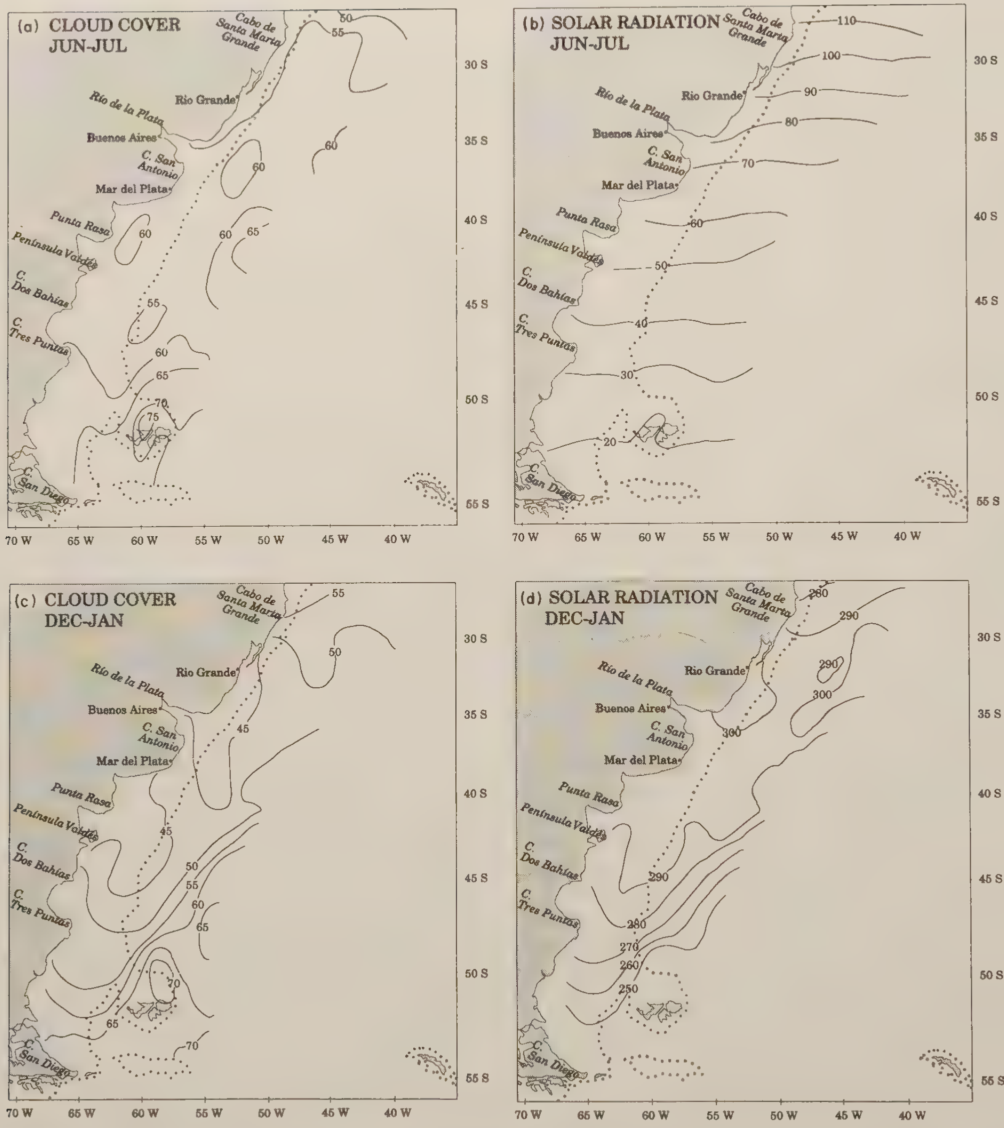
The summer pattern of solar radiation (Fig. 3d) available for absorption, either by water molecules to warm the upper ocean or by plant pigments to support organic production, is strongly affected by the cloud cover distribution. The vicinity of the Falkland Islands receives the lowest solar radiation in the region. The anchoita habitat, near the coast, receives a relatively larger flux of solar radiation entering the ocean than does the area further offshore.

Sea-surface temperature

The pattern of sea-surface temperature (Fig. 4) is dominated by the major boundary flows of the region. These advective effects are large enough so that, other than the global-scale poleward temperature decrease, effects of the pattern of direct solar heating (Fig. 3b, d) are effectively masked. The effect of the warm poleward-flowing Brazil Current is seen in the tongue-like southwestwardly contortions of the isotherms in the northern portion of the region. Oppositely orientated tongue-like features mark the cold equatorward-flowing Falkland Current which dominates the pattern in the mid-portion of the gridded region. There is an impression of a "collision" of these two massive boundary current flows in the area off the Río de la Plata (Gordon and Greenglove, 1986; Olson *et al.*, 1988), with the Brazil Current flow being deflected offshore and the Falkland Current appearing to slide inshore of the Brazil Current to take on the character of a coastal counterflow. Also, inshore of the Falkland Current various instances of recurvature of the isotherms, particularly in the area of ~40°S to ~45°S latitude, suggest some degree of coastal counterflow in the poleward direction over the mid-shelf.

Wind mixing index

We estimate the intensity of input of mechanical energy by the wind, which would then become available for turbulent mixing of the upper ocean, by means of a "wind mixing index", which is the mean value of the third power (cube) of the wind speed (see Appendix). In our region of interest (Fig. 5), values of this index are very much higher in the offshore region than in the band lying within several hundred kilometers of the coast. A local maximum tends to


(a) CLOUD COVER JUN-JUL
(b) SOLAR RADIATION JUN-JUL
(c) CLOUD COVER DEC-JAN
(d) SOLAR RADIATION DEC-JAN
Cabo de Santa Marta Grande
Rio Grande
Rio de la Plata
Buenos Aires
C. San Antonio
Mar del Plata
Punta Rasa
Peninsula Valdes
C. Dos Bahias
C. Tres Puntas
C. San Diego
50
55
60
65
70
75
110
100
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80
70
60
50
40
30
20
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280
290
300
270
260
250
30 S
35 S
40 S
45 S
50 S
55 S
70 W
65 W
60 W
55 W
50 W
45 W
40 W

Figure 3. Mean cloud cover and solar radiation. (a) Cloud cover during June–July (austral winter); (b) solar radiation absorbed through the sea surface during June–July; (c) cloud cover during December–January (austral summer); (d) solar radiation absorbed through the sea surface during December–January. Units for cloud cover distributions are percent of sky obscured. Units for solar radiation distributions are watts m^{-2} (to convert to cal cm^{-2} day^{-1}, multiply by the factor 2.064). The dotted line indicates the continental shelf limit (200 m isobath).

be found in the latitude band from about 38° to 45°S, about 600 km offshore. Parrish *et al.* (1983) found that, with the exception of the South African population, the major anchovy populations of eastern ocean boundary regions (e.g. the anchoveta of north-central Peru, the anchoveta of southern Peru and northern Chile, the anchovy of Namibia, and the anchovy of the Southern California Bight) spawn under circumstances such that seasonal average wind mixing index values exceeding about 0.3 index units (one wind mixing index unit = 1000 m^3 s^{-3}) are avoided. Such low seasonal values of the index are generally absent off subtropical eastern South America, except perhaps in restricted areas directly sheltered by coastal topography. On the scales resolved by our one-

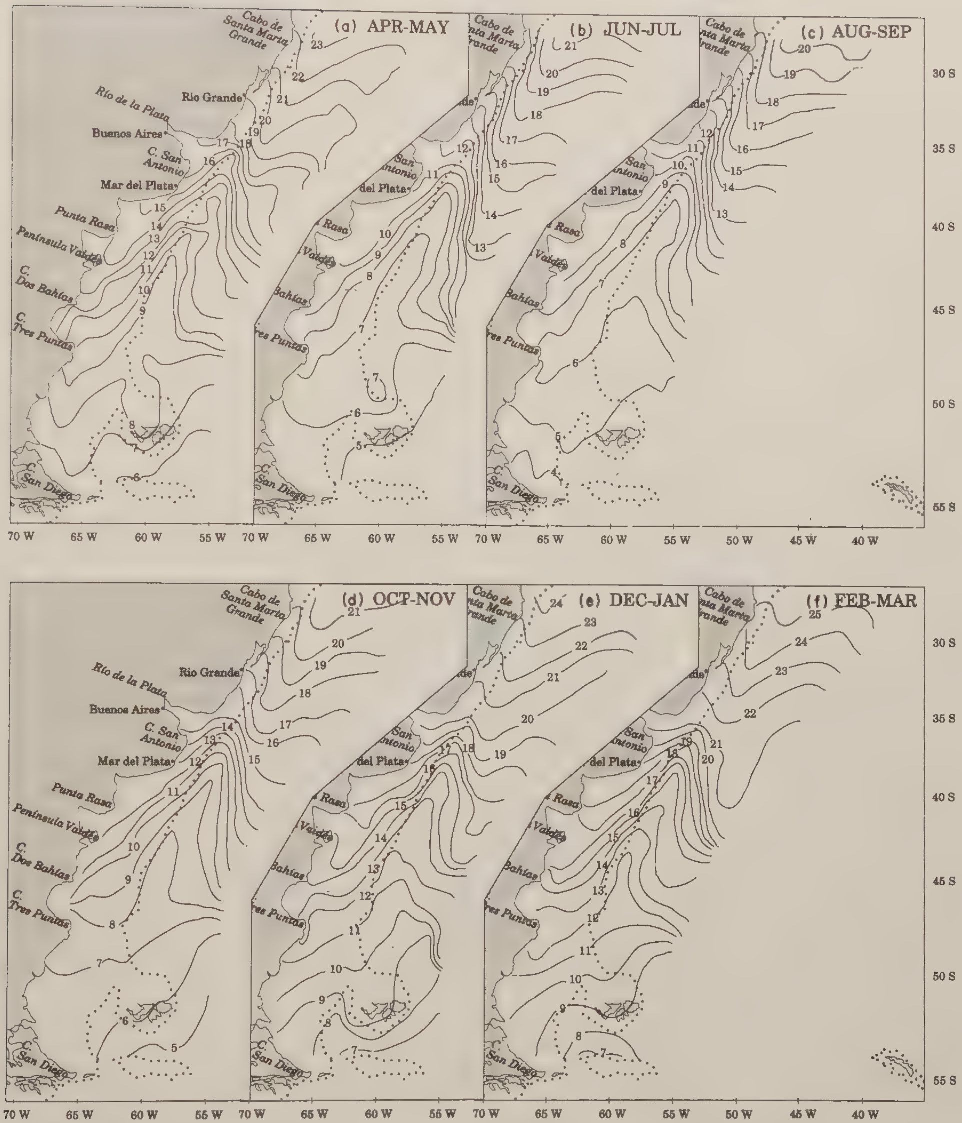
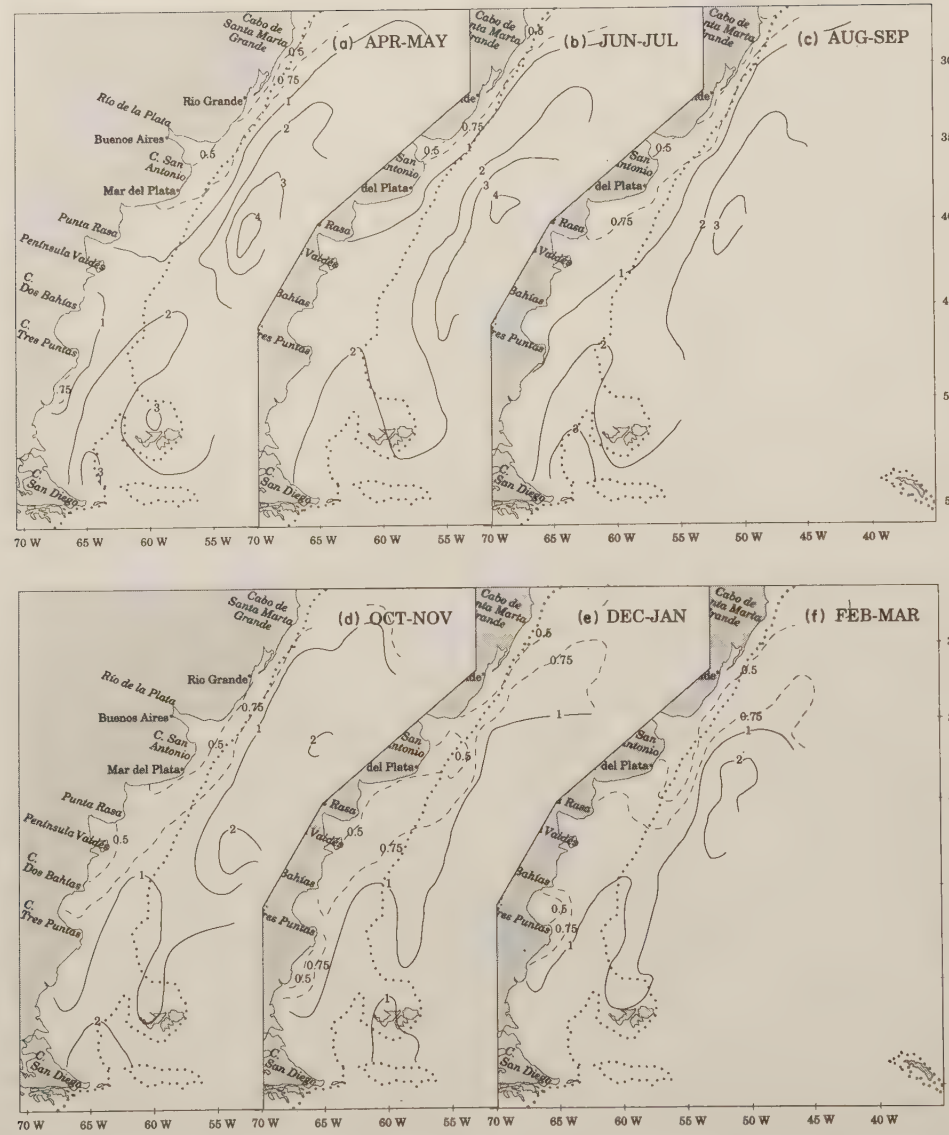

(a) APR-MAY
(b) JUN-JUL
(c) AUG-SEP
(d) OCT-NOV
(e) DEC-JAN
(f) FEB-MAR
Cabo de Santa Marta Grande
Rio Grande
Río de la Plata
Buenos Aires
C. San Antonio
Mar del Plata
Punta Rasa
Península Valdéz
C. Dos Bahías
C. Tres Puntas
San Diego
30 S
35 S
40 S
45 S
50 S
55 S
70 W
65 W
60 W
55 W
50 W
45 W
40 W

Figure 4. Sea surface temperature distributions for two-month segments of the seasonal cycle. Units are degrees Celsius. The dotted line indicates the continental shelf limit (200 m isobath). (a) April–May; (b) June–July; (c) August–September; (d) October–November; (e) December–January; (f) February–March.

degree areal summaries, minimum index values near the coast tend to fall only slightly below 0.5.

From late fall to early spring (Fig. 4a, b, c) the area within the 0.5 wind mixing index contour tends to be restricted to the far north of the region or to within the mouth of the Río de la Plata. However, during spring (Fig. 5d) the 0.5 contour encompasses an area off the stretch of coastline from near Rio Grande (~32°S) to somewhat southwest of Mar del Plata. To the south of Punta Rasa (~41°S) it reappears, encompasses Península Valdéz, and extends to the vicinity of Cabo Dos Bahías (~45°S). During early summer (Fig. 5e) the southward extremity (except for a disjoint segment south of Cabo Tres Puntos) of the 0.5 index value contour recedes northward to Península Valdéz (~43°S). By late summer to early fall (Fig. 5f), the area where seasonal values of the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C. San Antonio
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Punta Rasa
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C. Dos Bahias
C. Tres Puntas
C. San Diego
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40 S
45 S
50 S
55 S
70 W
65 W
60 W
55 W
50 W
45 W
40 W

Figure 5. "Wind cubed" index of rate of addition to the ocean, by the wind, of mechanical energy available for turbulent mixing of the upper water column; nominal units are $m^{-3} s^{-3}$. The dotted line indicates the continental shelf limit (200 m isobath). (a) April–May; (b) June–July; (c) August–September; (d) October–November; (e) December–January; (f) February–March.

wind mixing index are less than 0.5 has receded northward along the coast such that its southern limit lies near Mar del Plata (~38°S).

Subsurface stability structure

Except within the interior of the coastal bight (herein called the "Southeastern Brazilian Bight", after Matsuura, 1989) to the north of Cabo Santa Marta Grande (see Fig. 4 in BP), seasonal mixing index values substantially lower than 0.5 tend not to be available in the habitat of the anchoita. Thus, although the southerly extent of the anchoita's spawning habitat expands and contracts roughly in phase with the seasonal movement of the zone of relatively low wind mixing energy, spawning must largely take place at much higher rates of wind-derived mixing energy than the 0.05–

0.3 index values typical of anchovy reproductive habitats in eastern ocean coastal ecosystems (Parrish *et al.*, 1983). The only comparable example among the anchovy populations treated by Parrish *et al.* is the South African anchovy population, where index values exceeding 0.6 characterize the spawning habitat. Parrish *et al.* attribute the ability of the South African population successfully to reproduce under such energetic wind conditions to a protected stable layer formed at depth by the confluence of warm Indian Ocean surface water from the Agulhas Current with the cooler, more dense Atlantic source water of the Benguela Current (see also Shelton and Hutchings, 1990).

Off eastern South America, there exists a similar confluence of the warm tropical Brazil Current with the cool Falkland Current (Olson *et al.*, 1988), although the anchoita reproductive habitat extends far beyond the area directly affected by this confluence. To demonstrate characteristic subsurface structure in various areas of the habitat, we have assembled some schematic profiles of subsurface structure (Fig. 6) from available published sections (see caption for sources). These are constructed from contoured sections rather than from original data and in most cases are derived from a single cruise rather than a long-term climatological mean. We thus offer them merely as illustrations of the general types of structure to be found in particular regions and seasons.

During summer within the Brazilian Bight (Fig. 6a, c), very strong stability is built up in the upper water column by intrusion of deeper waters which upwell and spread across the continental shelf (Castro Filho *et al.*, 1987) and by surface heating and lack of turbulent mixing, particularly in the shoreward portion of the bight (Fig. 6a). Thus, during the late spring to early summer period there is strong stability and resistance to vertical mixing of the water column. Conversely, during winter the water in the shoreward half of the bight may be completely homogenized (Fig. 6b).

Off Uruguay and the extreme south of Brazil, subsurface stability over the continental shelf is strongest in the winter (Castello and Müller, 1977) due in large part to freshwater runoff from the continent; apparently, salinity controls the density structure to such an extent that at some locations on the shelf, temperature actually increases with depth during winter (Fig. 6f). Sizable winter spawning occurs in this region (Fig. 1). In addition, during the other seasons of the year, there continues to be substantial stability in the water column structure (e.g. Fig. 6e) as well as heavy spawning activity, which apparently (there are no published summer surveys) continues throughout the year.

Further south along the Argentine coast the situation reverses. Water column stability is strongest in summer (Fig. 6g) and may vanish completely in winter (Fig. 6h). Here spawning declines sharply during winter. However, in addition to poor stability conditions, the temperature in this region during winter (Fig. 6h) may fall below a level favorable for reproductive activity of *Engraulis* (see Discussion).

The Patagonian shelf, yet further to the south, is characterized by strong tidal mixing which in shallower areas may homogenize the whole water column. The result is occurrence during summer of shelf sea fronts (Simpson and Hunter, 1974; Hunter and Sharp, 1983), which are zones of convergence between mixed water on the shallower side (Fig. 6i) and stratified water offshore (Fig. 6j). Fronts of this type are strongly evident near Península Valdéz (Glorioso, 1987).

Surface Ekman transport

The seasonal progression of bimonthly distributions of surface Ekman transport, which represents the transport in the ocean surface layer responding to the seasonal variablity of wind stress (see Appendix), is displayed in Fig. 7. Strong surface convergence in a band from about 300 to 600 km offshore, due to the anticyclonic wind stress curl discussed in the subsection on wind stress, is obvious in the general decrease in vector symbol length in the direction of transport. The existence of surface convergence in the offshore area is in distinct similarity to eastern boundary current regions where anticyclonic wind stress curl at similar distances offshore (Nelson, 1977; Bakun and Nelson, 1991), and corresponding convergence of surface waters and organisms may provide particularly efficient feeding grounds for nektonic predators (Parrish *et al.*, 1981). Offshore of the convergent area there appears to be general divergence in the surface Ekman transport field.

Near the coast, the surface Ekman transport is generally directed toward shore, and so organisms of this region appear to be largely unaffected by the problem of chronic offshore Ekman transport of planktonic stages that seems to be a controlling aspect of spawning strategies in eastern boundary regions (Parrish *et al.*, 1981, 1983) or even in the more tropical region of the western South Atlantic (Bakun and Parrish, 1990). In fact the only incidence of substantial large-scale average offshore Ekman transport is from Cabo Santa Marta Grande (~28°S) to Rio Grande (~32°S) during the warmer half of the year (Fig. 7d, e, f). As noted earlier, there appears to be reduced anchoita spawning activity in the northern part of the range during summer and fall. This absence of the large-scale wind-driven offshore loss of reproductive products that is faced by pelagic spawners in upwelling systems is another feature in common with South African anchovies (*Engraulis capensis*) which migrate out of the Benguela upwelling system as young adults to join a spawning population positioned in an area adjacent to the Cape of Good Hope, where Ekman transport is characteristically directed toward the coast (Parrish *et al* 1983).

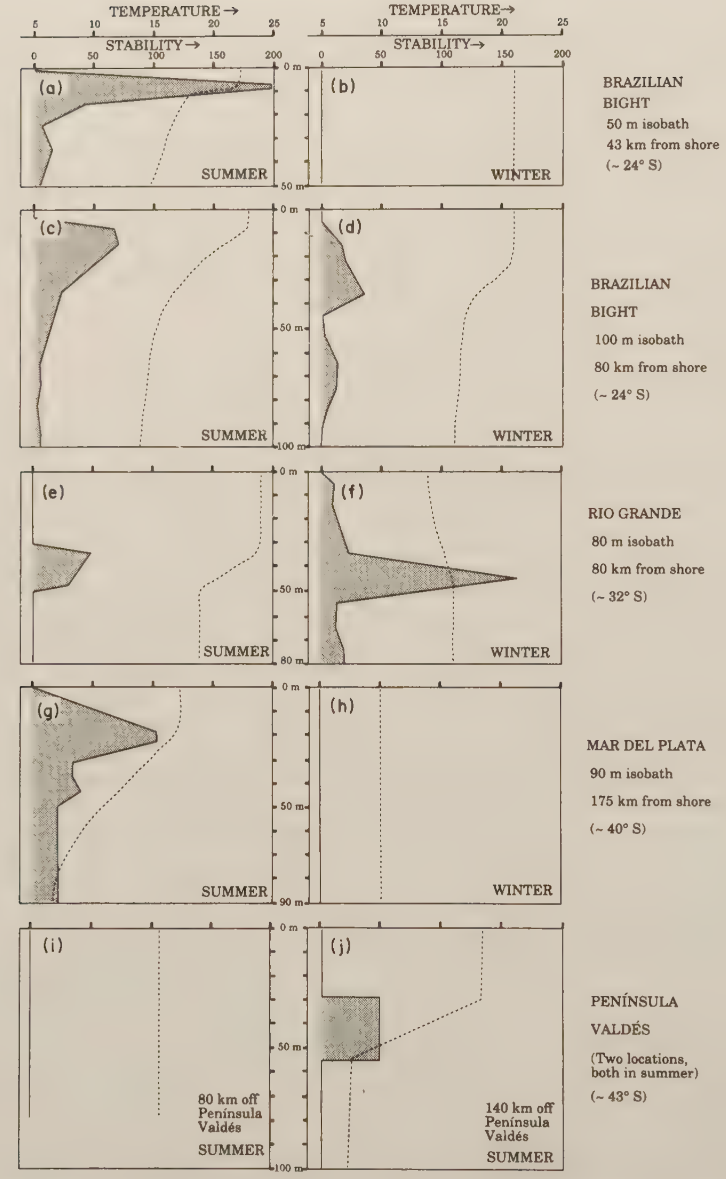
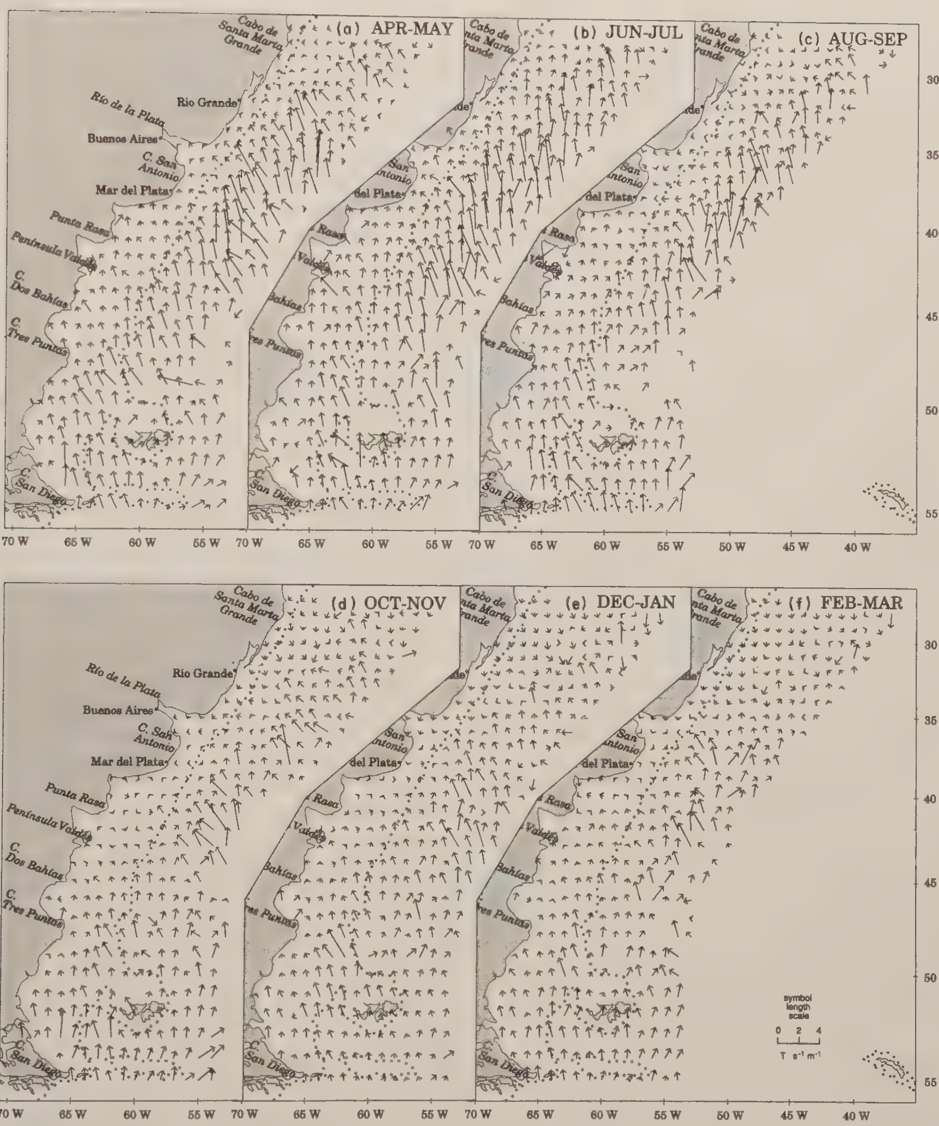


Figure 6. Vertical distributions of static stability ($10^{-3}d\sigma_t/dz$; m^{-1}) plotted as a solid line with shading, and temperature (°C) plotted as a dashed line. These distributions were drawn from published contoured profiles rather than from original data: (a, b, c, d) from Castro Filho *et al.* (1987); (e, f) from Castello and Müller (1977); (g, h) from Martos (1986); (i, j) from Glorioso (1987). Glorioso presented only temperature profiles; thus effects of salinity structure are neglected in panels (i) and (j).

Processes of nutrient enrichment

The only area within the anchoita habitat where sustained, locally wind-driven coastal upwelling occurs is the Cabo Frio–Cabo São Tomé upwelling center (described in BP) at the northern limit of the Brazilian Bight. The existence of enclosed gyral circulation patterns within the coastal indentation favors diffusion of the enriched surface waters, originating at the upwelling center, into the Bight area. In addition, vertical sections (e.g. Castro Filho *et al.*, 1987) suggest continued upwelling near the shelf break along the seaward boundary of the Bight area where frictional drag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symbol length scale
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Figure 7. Surface Ekman transport distributions for two-month segments of the seasonal cycle. Transport is proportional to vector symbol length. A symbol length scale is provided (panel g); units are metric tonnes per second across each meter width. The dotted line indicates the continental shelf limit (200 m isobath). (a) April -May; (b) June–July; (c) August–September; (d) October–November; (e) December–January; (f) February–March.

created by the Brazil Current flowing along the shelf edge would lead to locally subgeostrophic flow, a correspondingly unbalanced onshore–offshore pressure gradient, and resulting onshore transport in a bottom Ekman layer (Hsueh and O'Brien, 1971). During the austral spring and summer, there is also substantial wind-driven offshore Ekman transport at the seaward edge of the Bight area (see Fig. 3 in BP) available to drive wind-induced upwelling occurring at the shelf break (Huyer, 1976; Petrie, 1983).

To the south (i.e. in the bulk of the anchoita habitat), seasonal-scale offshore-directed wind-driven surface transport that would drive conventional coastal upwelling is largely lacking (Fig. 7), except for minimal amounts during summer extending only as far south as Rio Grande

(~32°S). However, shelf break upwelling continues to be highly evident in vertical hydrographic sections (e.g. Servicio de Hidrografía Naval, 1969) and in satellite imagery (Podesta, 1990), even in the area dominated by the northward flowing Falkland Current. Ekman transport near the sea floor due to bottom drag in such an equatorward western boundary current would be directed offshore, rather than in the onshore direction corresponding to upwelling. Podesta cites several potential mechanisms for shelf break upwelling in such a case. These include upwelling in small-scale eddies along the current edge (Paffenhöffer *et al.*, 1984), interactions between coastal trapped waves and bottom topography (Dickson *et al.*, 1980), and effects of interactions of internal tides with the shelf break and wind stress (Mazé *et al.*, 1986). In addition, Kinsella *et al.* (1987) describe a mechanism for onshore water movement in response to the Ekman suction caused by curl of the bottom stress in an equatorward western boundary flow.

Finally, tidal mixing over the shelf can have a similar effect to upwelling. In the resulting homogenized water column, nutrients and other properties associated with the denser lower layers of the previously stratified water are mixed into the illuminated upper layers where they are available for photosynthesis. Carreto and Benavides (in press) cite consistently greater availability of nitrates in the euphotic zone on the mixed side of the fronts near Península Valdéz, compared to the stratified side. They also note predominance of chain-forming diatoms (such as typify upwelling centers) on the mixed side and relative scarcity of phytoplankters (being mostly heterotrophic dinoflagellates) on the stratified side. They report that the largest phytoplankton concentrations occur in the transition zone between (i.e. associated with the convergent front). Based on studies of satellite imagery, Podesta (1990) states that the area influenced by these fronts, and also the area of the shelf-break front, are the only places on the Patagonian shelf where near-surface phytoplankton biomass remains high throughout the summer.

Discussion

The anchoita spawning habitat extends some 2800 km along the coast of South America (Fig. 1) and spans a broad range of environmental conditions. The range of actual[3] sea surface temperature (SST) at which *Engraulis* eggs occur is from 8.8°C to 23.2°C in Argentine waters (Sánchez, 1989), and from 16°C to 28°C in the Southeastern Brazilian Bight (Nakatani, 1982). This is similar to the overall range found in the California Current, 9°C to 27°C (Hernandez-Vasquez, 1991). According to Sánchez (1989) the temperature corresponding to maximum spawning incidence of *Engraulis* varies from 13.0°C in September to 18.5°C in February in Argentine waters; the corresponding values for California Current *Engraulis* are from 14.5°C in April to 18.7°C in September (Hernandez-Vasquez, 1991).

Most sampling of pelagic larvae is done via vertically integrating "oblique" tows, but occurrence or absence is usually, as in the studies cited above, compared to SST. Where there is a marked vertical temperature structure, SST may be a rather imprecise indicator of the temperature conditions in the depth zone actually occupied by the sampled larvae. Campaner and Honda (1987) state that in the Brazilian Bight (~23°–27°S) late winter anchoita spawning is scattered throughout the outer shelf where temperatures at depth are less than 20°C, whereas during the late spring to early summer, spawning is concentrated in cool upwelling regions south of Cabo Frio and near the coast. In the same region, Matsuura *et al.* (1985) found nearshore concentrations of adult anchovy in cool (15–20°C) upwelled water; in areas with a higher SST, anchovies were found in or beneath a shallow thermocline at temperatures of 15–19°C. Brewer (1976) determined temperature tolerances of larvae of California Current northern anchovy (*Engraulis mordax*) by controlled laboratory experiments. He found that some eggs hatch at any temperature between 8.5° and 28.5°C and that the larval temperature tolerance range extends from 7° to 30°C. However, the proportion of larvae which developed in a normal manner decreased when temperatures fell below 11.5°C or exceeded 27°C.

From the information available, the reproductive habitat temperature tolerance of *Engraulis anchoita* does not therefore appear to differ substantially from that of eastern ocean boundary region populations of the genus *Engraulis*. In fact, the spawning habitat temperature range of this one species, in terms of long-term seasonal mean SST, essentially encompasses the combined temperature ranges of all the eastern ocean populations examined by Parrish *et al.* (1983). Therefore, we find in the case of the anchoita no reason to modify the conclusion, reached by Parrish *et al.* (1983) with respect to eastern ocean anchovies (and also sardines), that selection of spawning habitat for any particular optimum temperature may be less important than the striking of a beneficial balance of physical processes affecting water column stability, retention of reproductive products within a favorable habitat, and nutrient enrichment leading to adequate production of appropriate larval food particles.

The most common manner of striking this balance, noted by Parrish *et al.*, is in an environmental configuration wherein spawning grounds are located within coastal indentations downstream of coastal upwelling centers. The upwelling provides enrichment to the food web, the products of which diffuse into the coastal bight where the strong offshore Ekman transport characteristic of upwelling regions relaxes and semi-enclosed gyral circulation patterns aid retention of larvae within the bight area. Due to the sheltering effect of the coastal topography, wind-mixing falls to very low values within these indentations, allowing formation of the fine-scale food particle concentrations favoring successful larval feeding. The archetype of this pattern is the Southern California Bight, which constitutes the major spawning grounds of the northern anchovy (*Engraulis mordax*) and also, prior to its population collapse, of the Pacific sardine (*Sardinops sagax caerulea*). This pattern also applies in more or less degree to the anchoveta (*Engraulis ringens*) and sardine (*Sardinops sagax sagax*) populations spawning off southern Peru and northern Chile, to the sardine (*Sardina pilchardus*) stocks of the Canary Current system spawning in coastal bights near Casablanca and near Ifni, and to the anchovies (*Engraulis capensis*) and sardines (*Sardinops sagax ocellatus*) spawning near Palgrave Point in Namibia.

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[3] As opposed to long-term seasonal mean values, as displayed in Fig. 4.

Bakun and Parrish (1990) show a nearly identical configuration (Fig. 8a) for the spawning habitat of the Brazilian sardine (*Sardinella aurita*), a sardine-type fish of a more tropical genus than the *Sardinops* and *Sardina* species inhabiting subtropical eastern ocean upwelling systems. This population shares the Brazilian Bight spawning habitat with the northernmost segment of the anchoita population.

In the bulk of the anchoita habitat to the south, this particular configuration is not available. Surface Ekman transport tends to be directed onshore (Fig. 7), which is opposite to the direction that would induce coastal upwelling. However, the hydrographic situation of this wide, abruptly breaking continental shelf generates substantial upwelling at the shelf break (see previous section). The onshore Ekman transport would serve to carry the upwelling-based nutrients and enriched production onto the inner shelf habitat, where the continent itself serves as a shield from the large-scale westerly winds and relatively low wind-mixing rates result (Fig. 5). Under these conditions, relatively strong water column stability (Fig. 6e, f, g) is favored by confluence of different water masses associated with the various alongshore boundary flows, by strong seasonal surface heating in the wind sheltered region, and by substantial fresh water input. South of Mar del Plata, where water column stability disappears during winter (Fig. 6h), no substantial winter spawning is reported, although as discussed above we cannot isolate this finding from a possible effect of temperature. The areas of water mass confluence, including fronts associated with the freshwater outflows, represent convergence zones which may serve to concentrate distributions of larval food particles. Certainly the onshore-directed surface Ekman transport facilitates the retention of eggs and larvae within the shelf habitat. Thus, it appears that in quite a different configuration (Fig. 8b) to the common one for upwelling regions (Fig. 8a), the various processes combine to yield quite similar conditions for successful reproduction. This second configuration would seem to have its strongest analog in the spawning grounds of the South African anchovy population (Parrish *et al*., 1983).

Toward the southern end of the reproductive habitat of the anchoita, notably in the vicinity of Península Valdéz (see previous section), strong tidal mixing over the very wide Patagonian shelf results in a third configuration (Fig. 8c). Over the shallower areas, tidal energy is sufficient to overcome the potential energy of the stratified water column and the water may become mixed from top to bottom. Nutrients that otherwise would have been held in the denser bottom layer are mixed upward into the illuminated surface layers to support photosynthetic production. In the homogenized area, the mixed water column is more dense at the surface and less dense at depth compared to water at the same depth in the stratified area offshore. Thus, surface water from the stratified region would tend to override the heavier mixed water, resulting in shoreward surface flow toward a convergent front at the sea surface; the mixed water would tend to sink under the front and flow offshore beneath the surface layer (Fig. 8c). At the bottom, the more dense water from offshore would tend to push shoreward to displace the less dense mixed water. These interleaving flows of different densities form a stable thermocline layer flowing slowly offshore from the frontal zone.

Within this mid-depth layer, the several conditions common to the other two configurations (i.e. those illustrated in Fig. 8a and b) would appear to be well realized. Flow from a zone of enrichment (the mixed zone) may carry resultant production of food particles (e.g. developmental stages of calanoid copepods which appear to be the principal dietary items of both larval and juvenile anchoita (Ciechomski, 1967)) into a zone of stability (the mid-depth thermocline). Convergence within the frontal zone may intensify formation of concentrated patch structure, which is buffered from turbulent dispersion due to tidal friction at the bottom by the denser layer beneath and from wind-generated turbulence by the less dense layer above. Retention of larvae within the coastal habitat may be aided by appropriate vertical migratory behavior. For example, excursion into either the upper layer or the lower layer, either on a diel basis or in the course of ontogenetic development, would tend to counter the general offshore movement within the mid-depth layer (Bakun, 1989). Whether or not adaptive vertical migration is actually involved, the Patagonian shelf is so wide (more than 350 km in width off Península Valdéz) that the layered circulations associated with shelf sea fronts near the coast must surely decay within a small fraction of the total distance to the offshore limit of the continental shelf habitat. The large-scale onshore wind-driven Ekman transport, tending to impede drift off the shelf, becomes abruptly stronger with distance from the coast (Fig. 7).

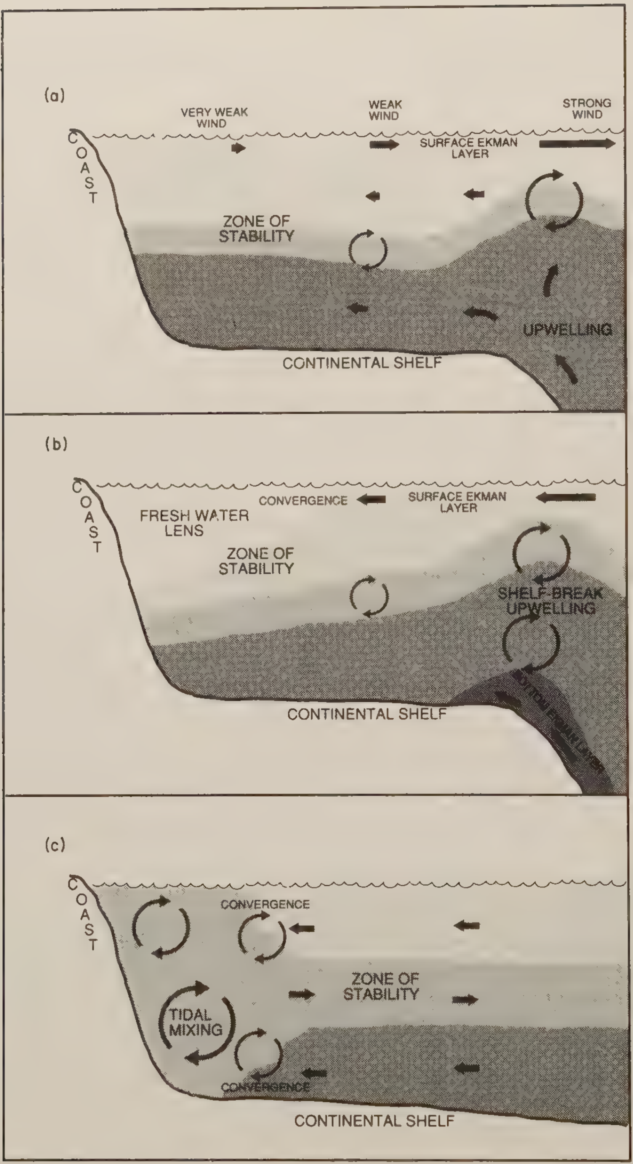
(a)
VERY WEAK WIND
WEAK WIND
STRONG WIND
COAST
SURFACE EKMAN LAYER
ZONE OF STABILITY
UPWELLING
CONTINENTAL SHELF
(b)
COAST
CONVERGENCE
SURFACE EKMAN LAYER
FRESH WATER LENS
ZONE OF STABILITY
SHELF-BREAK UPWELLING
BOTTOM EKMAN LAYER
CONTINENTAL SHELF
(c)
COAST
CONVERGENCE
ZONE OF STABILITY
TIDAL MIXING
CONVERGENCE
CONTINENTAL SHELF

Figure 8. Schematic diagrams of environmental configurations prominent in spawning strategies of *Engraulis anchoita*. Heavier shading connotes greater water density. Wider arrows indicate mean water transport; lengths are scaled to suggest relative magnitudes. Linked circular pairs of arrows indicate mixing processes; their sizes are scaled to suggest relative intensities of mixing: (a) Within a coastal indentation in a wind-driven coastal upwelling regime (i.e. the Brazilian Bight; also descriptive of the Southern California Bight in the northeastern Pacific and other eastern ocean anchovy habitats). (b) Onshore wind-driven transport over a wide continental shelf with upwelling at the shelf break and freshwater runoff from the continent (i.e. extreme north coast of Argentina, coast of Uruguay and Brazilian coast to north of Rio Grande). (c) A shelf-sea front system driven by tidal mixing (i.e. the Patagonian shelf in the vicinity of Península Valdéz; also descriptive of similar frontal systems in the North Sea, the Gulf of Maine, etc.)

This third configuration (Fig. 8c) has been previously indicated (Iles and Sinclair, 1982; Sinclair, 1988) as being prominent in the spawning habitat of herring (*Clupea*) in high latitude shelf-seas such as the Gulf of Maine, the North Sea, etc. Also, Buckley and Lough (1987) report that haddock larvae (*Melanogrammus aeglefinus*) are found to be much more numerous and faster growing in the thermocline zone immediately offshore of the tidally-mixed area over Georges Bank than in either the surface waters or at any depth within the mixed area.

Conclusions and speculative remarks

The example of the anchoita thus demonstrates the extreme versatility of anchovies. Evidently, one extended population encompasses the combined reproductive temperature ranges of all the eastern ocean populations examined by Parrish *et al.* (1983). It also uses both classes of environmental configurations shown in that study as fostering successful anchovy reproduction in eastern ocean ecosystems. In addition, in the very wide Patagonian shelf habitat, the anchoita evidently utilizes a configuration similar to one used by herring in the wide shelf-sea ecosystems of boreal high latitudes. The anchoita is also successful in substantially co-inhabiting, by partitioning habitat space according to temperature preference, the spatial area which constitutes the primary habitat of the Brazilian sardine, a more tropical species.

One might speculate whether this evident "plasticity" with respect to external conditions could be a major reason for the remarkable success of the genus *Engraulis* worldwide. For example, the anchoveta (*Engraulis ringens*) of the Peru Current was, before exploitation, by far the largest single fish population ever known to inhabit a coastal ecosystem. It also appears to have largely remained the overwhelmingly dominant component of the Peru Current ecosystem for millennia (DeVries and Pearcy, 1982), rather than to have suffered periodic displacement by the somewhat longer-lived sardines, as apparently has occurred in other systems (Soutar and Isaacs, 1969; Shackleton, 1987). We might note that the recent expansion of sardines in the Peru Current system came only after enormous exploitation had contributed to the collapse of the anchoveta population. An explanation for the spectacular success of the anchoveta might be the very fact that the Peru system, being geographically situated so as to bear the full brunt of global scale El Niño–Southern Oscillation phenomena, is uniquely subject to intermittent drastic environmental rearrangement. These disruptions could give the advantage to the Peruvian anchoveta over more specialized (e.g. demersal) species which are able to establish and maintain themselves in other ecosystems, feeding at a somewhat higher trophic level (i.e. less efficiently with respect to the primary organic production of the ecosystem) than anchovies, while suppressing the growth of lower trophic level populations through their incessant predation. In an ecosystem relatively free of such less productive predatory components, much larger biomasses might be attained by a low trophic level species having a short life cycle and rapid population responses.

In summary, our various examinations of seasonality and geography of anchovy reproductive activity have yielded a rather consistent picture of quite a simple combination of environmental factors. First, we consistently find enhanced enrichment of the food web via physical processes (upwelling, etc.). Second, there is opportunity for concentrated patches of food particles to accumulate (i.e. by means of stability, lack of active turbulent mixing, and/or strong convergence in frontal structures). Finally, there is available some mechanism promoting retention of reproductive products within the near-coastal habitat. Areas where this combination does not exist, such as directly within "core" zones of maximal coastal upwelling, appear to be avoided in anchovy spawning habits. Any coastal marine ecosystem having an appropriate balance of this combination of factors, as long as temperature and other physiological factors fall within the species tolerances, would seem to be an appropriate habitat for a substantial anchovy population. Exceptions may be systems where long-period temporal irregularity may be mild enough to allow more specialized species to gain the upper hand. Likewise, in systems characterized by large-scale spatial irregularity (i.e. where the combination of factors supporting successful reproduction may exist in only limited subareas), the advantage may shift toward species more adapted for migration between adult feeding grounds and the reproductive habitat. One might speculate that the California Current system, where pelagic fishes spawn mainly within the Southern California Bight but migrate long distances to adult feeding grounds (Parrish *et al.*, 1981), might tend toward this latter situation. In the California system the more migratory sardines appear often to have been dominant over anchovies (Shackleton, 1987).

Off subtropical eastern South America, we see appropriate combinations of the several factors spread, in several different configurations, over a vast stretch of coastal ocean habitat. Accordingly, *Engraulis anchoita* dominates its trophic level in the coastal ecosystem of the southeastern Atlantic over the entire latitude band where temperatures are within its physiological tolerances. However, because various factors, including the very wide continental shelf area, relative absence of strong environmental perturbation, less dispersion than in certain other systems, etc., allow maintenance of large populations of predators (hake, squid, etc.), the anchoita itself may not approach the maximum total biomass that has been achieved by its relative on the western side of the continent. However, it is without question a key component of the trophic structure of this vast and enormously rich shelf-sea ecosystem.

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References

Bakun, A. 1985. Comparative studies and the recruitment problem: Searching for generalizations. CalCOFI Rep., 26: 30–40.

Bakun, A. 1989. L'ocean et la variabilité des populations marines. *In* L'Homme et les Écosystems Halieutiques, pp. 155–187. Ed. by J. P. Troadec. IFREMER, Brest. 817 pp.

Bakun, A., and Nelson, C. S. (1991) The seasonal cycle of wind stress curl in subtropical eastern boundary current regions. J. Phys. Oceanogr. (In press, Sept. 1991 issue).

Bakun, A., and Parrish, R. H. 1982. Turbulence, transport, and pelagic fish in the California and Peru Current systems. CalCOFI Rep., 23: 99–112.

Bakun, A., and Parrish, R. H. 1990. Comparative studies of coastal pelagic fish reproductive habitats: the Brazilian sardine (*Sardinella aurita*). J. Cons. int. Explor. Mer., 46: 269–283.

Brewer, G. D. 1976. Thermal tolerance and resistance of the northern anchovy *Engraulis mordax*. Fish. Bull. US, 74: 433–445.

Buckley, L. J., and Lough, R. G. 1987. Recent growth, biochemical composition, and prey field of larval haddock (*Melanogrammus aeglefinus*) and Atlantic cod (*Gadus morhua*) on Georges Bank. Can. J. Fish. aquat. Sci., 44: 14–25.

Companer, A. F., and Honda, S. 1987. Distribution and cooccurrence of *Calanoides carinatus* and larvae of *Sardinella braziliensis* and *Engraulis anchoita* over the southern Brazilian continental shelf. Bolm. Inst. oceanogr., S. Paulo, 35(1); 7–16.

Carreto, J. I., and Benavides, H. R. 1989. Phytoplankton. *In* Annex V, Synopsis on the reproductive biology and early life history of *Engraulis anchoita* and related environmental conditions in Argentine waters, pp. 2–3. Second IOC Workshop on Sardine/Anchovy Recruitment Project (SARP) in the Southwest Atlantic. IOC Workshop Report, 65. Unesco, Paris.

Castello, J. P. 1989. Synopsis on the reproductive biology and early life history of *Engraulis anchoita* and related environmental conditions in Argentine waters. Annex VII, 7 pp. *In* Second IOC Workshop on Sardine/Anchovy Recruitment Project (SARP) in the Southwest Atlantic. IOC Workshop Report, 65. Unesco, Paris.

Castello, J. P., and Müller, O. O., Jr. 1977. Sobre as condições oceanográficas no Rio Grande do Sul. Atlântica, 2(2): 25–110.

Castro Filho, B. M. de, Miranda, L. B. de, and Miyao, S. Y. 1987. Condições hidrográficas na plataforma continental ao largo de Ubatuba: variações sazonaiss e em média escala. Bolm Inst. Oceanogr., São Paulo, 35(2): 135–151.

Ciechomski, J. D. de. 1967. Investigations on food and feeding habits of the Argentine anchovy *Engraulis anchoita*. CalCOFI Rep., 11: 72–80.

Ciechomski, J. D. de, and Sánchez, R. P. 1986. Problematica del estudio de huevos y larvas de anchoíta (*Engraulis anchoita*) en relacion con la evolucion de sus efectivos pesqueros. I Resena de viente anos de investigacion. Publ. Com. Tec. Mix. Fr. Marl. 1(1): 93–109.

Cury, P., and Roy, C. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. Can. J. Fish. aquat. Sci., 46: 670–680.

DeVries, T. J., and Pearcy, W. G. 1982. Fish debris in sediments of the upwelling zone off central Peru: a late Quaternary record. Deep-Sea Res., 28: 87–109.

Dickson, R. R., Gurbutt, P. A., and Pillai, V. N. 1980. Satellite evidence of enhanced upwelling along the European continental slope. J. Phys. Oceanogr., 10: 813–819.

Ekman, V. M. 1905. On the influence of the earth's rotation on ocean currents. Ark. Mat. Astron. Fys., 2(11): 1–55 (reprinted in J. Cons. int. Expl. Mer, 20(2), 1954).

FAO. 1990. FAO yearbook of fishery statistics, Vol. 66, 1988. Food and Agriculture Organization of the United Nations. 502 pp.

Glorioso, P. 1987. Temperature distribution related to shelf-sea fronts on the Patagonian Shelf. Continental Shelf Res., 7: 27–34.

Gordon, A. L., and Greenglove, C. L. 1986. Geostrophic circulation of the Brazil–Falkland confluence. Deep-Sea Res., 33: 573–586.

Hernandez-Vasquez, S. 1991. Pattern analysis of abundance and geographical distribution of sardine (*Sardinops sagax caerulea*) and anchovy (*Engraulis mordax*) eggs and larvae in the California Current: 1951–1989. PhD thesis, Centro de Investigaciones Cientifica y Educacion Superior de Ensenada, Ensenada, B. C., Mexico.

Hsueh, Y., and O'Brien, J. J. 1971. Steady coastal upwelling induced by an along-shore current. J. Phys. Oceanogr., 1: 180–186.

Hubold, G. 1982. Zur laichökologie der Südwestaltlantischen sardelle *Engraulis anchoita* (Hubbs und Marini, 1935) Dissertation zur Erlangung des Doktorgrades *der Mathematisch-Naturwissenschaftlichen Fakultät* der Christian-Albrechts-Universität zu Kiel.

Hunter, J. R., and Sharp, G. D. 1983. Physics and fish populations: shelf sea fronts and fisheries, pp. 659–682. *In* Proceedings of the expert consultation to examine changes in abundance and species composition of neritic fish resources. Ed. by G. D. Sharp and J. Csirke. FAO Fish. Rep., 291. 1224 pp.

Huyer, A. 1976. A comparison of upwelling events in two locations: Oregon and Northwest Africa. J. Mar. Res., 34: 531–546.

Iles, T. D., and Sinclair, M. 1982. Atlantic herring: stock discreteness and abundance. Science, 215: 627–633.

Kinsella, E. D., Hay, A. E., and Denner, W. W. 1987. Wind and topographic effects on the Labrador Current at Carson Canyon. J. Geophys. Res., 92: 10853–10869.

Lasker, R. 1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull. US, 73: 453–462.

Lasker, R. 1978. The relation between oceanographic conditions and larval anchovy food in the California Current: Identification of the factors leading to recruitment failure. Rapp. P.-v. Réun. Cons. int. Explor. Mer., 173: 212–230.

Lasker, R. 1988. Studies on the northern anchovy; biology, recruitment, and fishery oceanography, pp. 24–41. *In* Studies on fisheries oceanography. Proceedings of the 25th Anniversary Symposium "Fisheries and Fishery Oceanography in the Coming Century". Tokyo, 10–13 Nov., 1986, Japanese Society of Fishery Oceanography.

Mantero, G. 1989. Early life history, pp. 3–4. *In* Annex VI, Synopsis on the reproductive biology and early life history of

Engraulis anchoita and related environmental conditions in Argentine waters. Second IOC Workshop on Sardine/Anchovy Recruitment Project (SARP) in the Southwest Atlantic. IOC Workshop Report, 65. Unesco, Paris.

Martos, P. 1986. Dinamica oceanografica en la plataforma continental entre las latitudes de 38 y 42 S. Informe Final de Bece de Iniciación CONICET, Instituto Argentino de Oceanografia, Bahia Blanca, Argentina. 140 pp.

Matsuura, Y. 1989. Synopsis on the reproductive biology and early life history of the Brazilian sardine, *Sardinella braziliensis*, and related environmental conditions. Annex VIII, 8 pp. *In* Second IOC Workshop on Sardine/Anchovy Recruitment Project (SARP) in the Southwest Atlantic. IOC Workshop Report, 65. Unesco, Paris.

Matsuura, Y., Amaral, J. C., Sato, G., and Tamassia, S. T. J. 1985. Ocorrencia de peixes pelagicos e a estrutura oceanografica da regiao entre o Cabo de Sao Tome (RJ) e Cananeia (SP), em Jan-Fev/1979. Ser. Doc. Tecm., PDP/SUDEPE, Brasilia, no. 33, pp. 3–70.

Mayr, E. 1982. The growth of biological thought. Harvard Univ. Press, Cambridge, Mass. 974 pp.

Mazé, R., Camus, Y., and Le Tareau, J.-Y. 1986. Formation de gradient thermiques à la surface de l'océan, au-dessuss d'un talus, par interaction entre les ondes et le mélange dû au vent. J. Cons. int. Explor. Mer., 42: 221–240.

Mendelssohn, R., and Mendo, J. 1987. Exploratory analysis of anchoveta recruitment off Peru and related environmental series, pp. 294–306. *In* The Peruvian anchoveta and its upwelling ecosystems: three decades of change. Ed. by D. Pauly and I. Tsukayama. ICLARM Studies and Reviews 15. Instituto del Mar del Peru (IMARPE), Callao, Peru; Deutsche Gesellschaft fur Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines. 351 pp.

Nakatani, K. 1982. Estudos sobre os ovos e larvas de *Engraulis anchoita* (Hubbs & Marini, 1935) (Teleostei, Engraulidae) coletados na regiao entre Cabo Frio (23°S) e Cabo de Santa Marta Grande (29°S). Masters Thesis. Universidade de Sao Paulo.

Nelson, C. S. 1977. Wind stress and wind stress curl over the California Current. US Dep. Commer. NOAA Tech. Rep. NMFS SSRF-714. 87 pp.

Olson, D. B., Podesta, G. P., Evans, R. H., and Brown, O. B. 1988. Temporal variation in the separation of Brazil and Malvinas Currents. Deep-Sea Res., 35: 1971–1990.

Paffenhöffer, G.-A., Wester, B. T., and Nicholas, W. D. 1984. Zooplankton abundance in relation to state and type of intrusions onto the southeastern United States shelf during summer. J. Mar. Res., 42: 995–1017.

Parrish, R. H., Nelson, C. S., and Bakun, A. 1981. Transport mechanisms and reproductive success of fishes in the California Current. Biol. Oceanogr., 1: 175–203.

Parrish, R. H., Bakun, A., Husby, D. M., and Nelson, C. S. 1983. Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish reproduction, pp. 731–778. *In* Proceedings of the expert consultation to examine changes in abundance and species composition of neritic fish resources. Ed. by G. D. Sharp and J. Csirke. FAO Fish. Rep., 291. 1224 pp.

Peterman, R. M., and Bradford, M. J. 1987. Wind speed and mortality rate of a marine fish, the northern anchovy (*Engraulis mordax*). Science, 235: 354–356.

Petrie, B. D. 1983. Current response at the shelf break to transient wind forcing. J. Geophys. Res., 88: 9567–9578.

Podesta, G. P. 1990. Migratory pattern of Argentine hake *Merluccius hubbsi* and oceanic processes in the southwestern Atlantic Ocean. Fish. Bull. US, 88: 167–177.

Roy, C., Cury, P., Fontana, A., and Belvèze, A. 1989. Stratégies spatio-temporelles de la reproductiiion des Clupéidés des zones d'upwelling d'Afrique de l'Ouest. Aquat. Living Res., 2: 21–29.

Sánchez, R. 1989. Annex V. Synposis on the reproductive biology and early life history of *Engraulis anchoita*, and related environmental conditions in Argentine waters. *In* Second IOC Workshop on Sardine/Anchovy Recruitment Project (SARP) in the Southwest Atlantic. Montevideo, Uruguay, 21–23 August 1989.

Servicio de Hidrografía Naval. 1969. Datos y resultados de las Campañas "Pesquería". Pesquería V. Publicaciones del Proyecto de Desarrollo Pesquero No. 10/V. Mar del Plata, Argentina. 100 pp.

Shackleton, L. Y. 1987. A comparative study of fossil fish scales from three upwelling regions. S. Afr. J. mar. Sci., 6: 79–84.

Shelton, P. A., and Hutchings, L. 1990. Ocean stability and anchovy spawning in the southern Benguela Current region. Fish Bull. US, 88: 323–338.

Simpson, J. H., and Hunter, J. R. 1974. Fronts in the Irish Sea. Nature, 250: 404–406.

Sinclair, M. 1988. Marine populations: an essay on population regulation and speciation. University of Washington Sea Grant Program (distributed by University of Washington Press. Seattle and London). 252 pp.

Soutar, A., and Isaacs, J. D. 1969. History of fish populations inferred from fish scales in anaerobic sediments off California. CalCOFI Rep., 13: 63–70.

Spach, H. L. 1990. Estudo comparativo da distrbuicao espactemporal e de padroes de agregacao de ovos e larvas de *Harengula jaguana, 'Sardinella brasiliensis* (Clupeidae: Osteichthyes) e *Engraulis anchoita* (Engraulidae: Osteichthyes) na costa sudeste do Brasil. PhD Thesis. Universidade de Sao Paulo.

Weiss, G., Fiejo de Souza, J. A., and Santos, A. 1976. Contribuicao ao conheciemento dO ictioplancton marinha da plataforma sul do Brasil, Atlantica, Rio Grande, FURG/BOA, 1(1/2): 7–78.

Weiss, G., and Feijo de Souza, J. A. 1977. Desova invernal de *Engraulis anchoita* na costa sul do Brasil em 1970 e 1976. Atlantic, Rio Grande, 2(2): 5–24.

Appendix

(*This Appendix presents the "Methods" section from Bakun and Parrish (1990), slightly modified to apply to the present paper.*)

Maritime reports contained in the US National Climatic Center's file of surface marine observations (Tape Data Family – 11) were grouped by one-degree latitude/longitude areal quadrangles and by two-month segments of the calendar year. Estimates of the various quantities of interest were produced from each individual report. The average value of all the estimates in each of these groups of reports was taken as the expected value for the location and two-month seasonal segment. The vector quantities, wind stress and Ekman transport, were averaged by component (vector averaged). The one-degree quadrangles selected for these summaries are centered at intersections of a grid of even whole degrees of latitude and longitude, extending 12 degrees of longitude offshore of the coastal boundary. Editing of the data consisted only of a gross error check to ensure physically possible values. Wind speeds greater than 50 m s^{-1} (~100 knots) were discarded as non-representative.

The vector quantities (Figs 2 and 7) are displayed as discrete vector symbols, each value being formed from a data set that is independent of all other one-degree quandrangle and two-month seasonal segments. The standard errors of the means of the respective northward and eastward components of the vector averages have also been plotted and examined in this study. Particularly large standard errors are typical of the estimates in certain offshore portions of the gridded area, reflecting not only very low available data density in that part of the region but also highly energetic variability in actual conditions. The low degree of coherence among spatially adjacent values visible in that area of Figures 2 and 7 should thus be regarded as largely reflecting lack of stability of the estimates rather than as indicating real small-scale spatial differences in characteristic value.

In preparing the contoured maps of the scalar quantities (Figs 3, 4, and 5), some minimal spatial smoothing has been applied. A 3 by 3 gridpoint version of the median smoother (Tukey, 1977) was employed to deal with the intense "bull's-eyes" that largely obscured the underlying significant pattern in the more data-poor offshore areas. However, in cases where this procedure may have removed features which were similarly indicated by directly adjacent independent samples and which were judged to be real after examination of the standard errors of the individual sample means, the contours were subjectively adjusted to re-insert the features. The intention has been to avoid showing features that are determined by only a single estimate (i.e. shown only in one of the two-month, one-degree lat/long sample means).

Wind stress

In estimating the stress of the wind on the sea surface we follow the procedures established by Bakun *et al.* (1974). An estimate of the stress is formed from each wind report according to

$$\vec{\tau} = \rho C_D |\vec{v}| \vec{v} \qquad (A.1)$$

where $\vec{\tau}$ represents the stress vector, ρ is the density of air (considered constant at 0.00122 gm cm^{-3}), C_D is an empirical drag coefficient (considered constant at 0.0013), $|\vec{v}|$ is the scalar wind speed, and $\vec{v}$ is the vector wind velocity. Reports where the wind direction is coded as "variable" are incorporated as calms (zero wind speed) in the stress summaries (see discussion by Bakun, 1987).

Ekman transport

On the seasonal time scales being addressed, the drift of waters at the sea surface under the direct action of the wind stress is satisfactorily characterized by the simplified idealization known as Ekman transport (Ekman, 1905). The net Ekman transport, $\vec{E}$, integrated over the layer of some several tens of meters beneath the sea surface in which it occurs, is given by

$$\vec{E} = \vec{k} \times \frac{\vec{\tau}}{f} \qquad (A.2)$$

where $\vec{k}$ is a unit vector directed vertically upward, "×" denotes the vector ("cross") product, τ is the wind stress vector and f is the Coriolis parameter ($f = 2\omega \sin \varphi$) where ω is the angular velocity of the earth's rotation and φ is the latitude (negative degrees in the southern hemisphere). Net Ekman transport is thus directed perpendicularly to the left of the wind stress in the southern hemisphere.

Wind mixing index

The rate at which the wind imparts mechanical energy to the ocean to produce turbulent mixing of the upper water column is roughly proportional to the third power, or "cube", of the wind speed (Elsberry and Garwood, 1978). A "wind mixing index", which is simply the mean of the cube of the observed wind speeds in each of the seasonal/areal samples, provides a guide to the variability in this particular process (Bakun and Parrish, 1982). In this case wind reports with the direction coded as "variable" are handled differently than in the stress summaries. Here the wind speed enters as a scalar quantity and directionality is immaterial, and so the wind speed value is incorporated directly as coded in the report.

Solar radiation

Net incoming solar radiation, Q_s, absorbed by the ocean was estimated from each individual report according to Bakun's (1987) adaptation of Nelson and Husby's (1983) computational procedure. The procedure is based on the standard formulation

$$Q_s = (1 - \alpha) Q_0 (1 - 0.62\, C + 0.0019\, h) \qquad (A.3)$$

where α is the fraction of incoming radiation reflected from the sea surface, Q_0 is the sum of the direct and diffuse radiation reaching the ground under a cloudless sky, C is the observed total cloud amount in tenths of sky covered and h is the noon solar altitude. Q_0 is estimated according to the procedures and tables presented by List (1949), using a 4 × 4 element curvilinear interpolation of the table entries via Bessel's central difference formula and assuming the atmospheric transmission coefficient of 0.7 recommended by Seckel and Beaudry (1973). The linear cloud correction in Equation (3) is as suggested by Reed (1977); Reed's recommendation that no correction be made for cloud amounts less than 0.25 of total sky was followed. Sea surface albedo, α, was extracted from Payne's (1972) tables, following Nelson and Husby's (1983) algorithm which involves entering the tables with the 0.7 atmospheric transmission coefficient, reduced by a factor equal to the cloud correction applied in Equation (3), and with the mean daily solar altitude.

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The Comparative Approach: Latitude-dependence and Effects of Wind Forcing on Reproductive Success

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Abstract

Recent findings concerning the effects of wind forcing on reproductive success of coastal pelagic fishes are surveyed, including several intriguing results that invite explanation. These include (1) the remarkable apparent constancy, among widely differing geographical settings, of the "ideal" wind condition (or "optimal environmental window") yielded by empirical time series analysis, (2) a tendency for peak reproductive activity to coincide with the seasonal upwelling peak in low latitude locations but to be out of phase with the upwelling at higher latitudes, and (3) the remarkable capacity of the Peruvian ecosystem to support particularly massive pelagic fish populations. The latitudinal dependence of certain of the processes is introduced as a means of drawing conclusions via the comparative method. The importance of vertical and offshore scales is indicated. The concept of "scaled offshore velocity" is introduced. The interaction of latitudinal-varying factors with latitudinally-constant factors in near-equatorial latitudes is proposed as a hypothetical explanation of the special capacity of the Peru Current ecosystem with respect to pelagic fishes.

Résumé

De récents résultats concernant les effets du vent sur le succès de la reproduction des poissons pélagiques côtiers sont examinés et notamment certains faits curieux qui font l'objet d'un examen plus approfondi. On s'intéressera tout d'abord à la valeur de vent optimale pour le recrutement (ou "fenêtre environnementale optimale") qui apparaît constante quelque soit la région considérée; le second point concerne le calendrier de la reproduction qui semble être en phase avec la saison d'upwelling aux basses latitudes et décalé de quelques mois aux latitudes plus élevées. Pour terminer, une hypothèse concernant la capacité de l'écosystème péruvien à soutenir des populations de poissons pélagiques côtiers particulièrement importantes sera émise. La variation suivant la latitude de certains paramètres est ensuite envisagée comme un moyen permettant d'extraire des informations à partir d'une approche comparative. L'importance des échelles verticale et horizontale est soulignée. Le concept de "vitesse standardisée vers le large" est introduit. L'interaction entre des paramètres dépendant et indépendant de la latitude dans une zone proche de l'équateur est proposée comme hypothèse pour rendre compte de l'abondance des populations de poissons pélagiques devant les côtes du Pérou.

Introduction

Traditionally, temperature has been the variable of first choice in addressing environmental effects on fish populations. However, particularly with respect to the small pelagic-spawning clupeoid fishes that are the focus of the SARP project, recent findings have tended most often to implicate effects of wind acting on the sea surface. For example, a wind-based index of coastal upwelling (Bakun 1973) has been empirically related to population dynamics of a substantial number of commercial fish stocks of the California Current and other eastern ocean upwelling systems (Bakun and Parrish1980; Shepard *et al.*1984; Bakun 1985; Bakun in press). The work of Lasker (1975,1978,1988) has drawn attention to the detrimental effects of wind-induced turbulent mixing of the water column in dispersing fine-scale concentrations of food particles necessary for adequate larval nutrition. Peterman and Bradford (1987) have added support to Lasker's findings by empirically relating interyear variability in larval anchovy mortality rate off California to frequency of calm periods of sufficient duration for fine scale strata of food organisms to form. On the other hand, Rothschild and Osborn (1988) suggest that certain levels of turbulence could actually enhance feeding efficiency of small marine organisms. In a variant of Sinclair's (1988) "member/vagrant" hypothesis, Parrish *et al.* (1981) implicate detrimental effects of wind-induced offshore Ekman transport, which would carry eggs and larvae away from the favorable coastal habitat; Parrish *et al.* (1983) show a pervasive tendency for both offshore transport and exposure to turbulence to

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be minimized in reproductive habits of eastern ocean coastal pelagic fishes. Cury and Roy (1989) have extended these results by comparative time series analysis, employing new nonlinear methods (Mendelssohn and Cury 1987), and have empirically demonstrated a consistent "optimal environmental window", where reproductive success is favored at an intermediate range of wind speed, neither too low for adequate upwelling-based enrichment nor so high that excessive offshore transport and turbulent mixing occurs. Roy (1990) showed the same pattern of apparent selection for an intermediate ideal characteristic wind speed in a survey of the reproductive habits of West African coastal pelagic fishes.

The emergence of wind effects as perhaps the key environmental variable to be considered in the SARP context is particularly interesting with respect to the climate change problem. The need for insight as to consequences of global climate change has emerged as a key scientific issue throughout the world, and potential effects on marine ecosystems and resources are important and particularly uncertain issues. One "greenhouse effect" about which we can be rather certain is an increase in temperature contrast between the heated continental land masses and the oceans during the warmer seasons of the year. This would lead to amplified sea breeze circulations and alongshore coastal winds, correspondingly enhanced offshore Ekman transport in the ocean surface layer, and intensified coastal upwelling (Bakun, 1990).

The comparative method has been identified as a key component of the international SARP research strategy. In the following sections of this paper, we discuss certain recent results concerning wind-related effects on reproductive success of small coastal pelagic fishes. We use this discussion to introduce certain concepts and terminology that may be useful in drawing comparative inferences and in integrating the operational and "inferential" (Anon. 1983) approaches within the SARP project.

Latitude-Dependent Dynamics and Comparative Ecology

Many dynamic characteristics of the ocean-atmosphere system are dependent on latitude. This certainly applies to upwelling ecosystems. For example, eastern ocean coastal upwelling seasons continue essentially through the entire year near the tropics, but with increasing latitude they become increasingly restricted to a narrowing period in the "high sun" portion of the year (Wooster and Reid 1963; Parrish *et al.*1983). Within the upwelling season, the upwelling process which is rather steady in the tropics becomes increasingly variable and episodic with increasing latitude (Parrish *et al.* 1981). Since the local horizontal plane (i.e., tangent to the earth's surface) makes different angles to the earth's axis of rotation at different latitudes, the Coriolis constraint, which controls the observed effects of large-scale hydrodynamical linkages, depends very strongly on latitude. In fact, the Coriolis constraint vanishes at the equator, creating singularities in several crucial processes which have dynamic expressions with Coriolis effect in the denominator. Very significantly, the quantitative coupling of the momentum transferred from wind stress on the sea surface to transport of ocean surface water is very strongly a function of latitude, i.e.

$$\mathcal{E} = \frac{\tau}{f} \qquad (1)$$

where $\mathcal{E}$ represents the surface ocean Ekman transport (Ekman 1905), τ is the stress of the wind on the sea surface and f is the Coriolis parameter ($f = 2\Omega\sin\phi$, where Ω is the angular velocity of the earth and ϕ is the latitude; for convenience, we define $\mathfrak{f} = f/2\Omega = \sin\phi$; thus $\mathfrak{f} \sim f$, where "~" signifies "proportional to"). Thus $\mathcal{E} \sim \mathfrak{f}^{-1}$ (curve "D" in Fig. 1), and the Ekman transport responding to a given intensity of wind stress becomes exponentially large as the equator is approached. Note that when the wind stress is alonghore (equatorward on an eastern ocean coastal boundary, poleward on a western ocean boundary), $\mathcal{E}$ represents both the large-scale offshore transport of the ocean surface layer (and entrained larvae, etc.) and the locally wind-driven coastal upwelling.

Such strong dependences on latitude should be useful in sorting out the processes controlling spawning strategies and, by implication, reproductive success. For example, the latitude dependence might provide insight into the relative roles of turbulence and offshore transport in regulating larval survival, since the input of turbulent mixing energy at a given wind intensity is not believed to be dependent on latitude (Fig. 2).

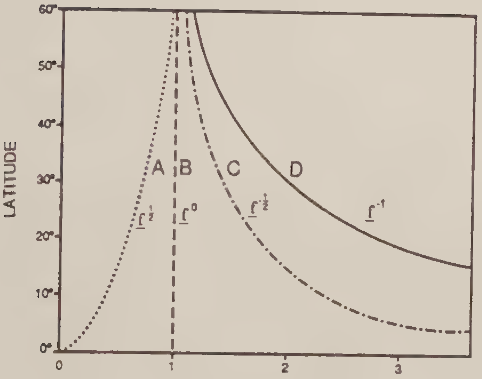

Figure 1. Latitude dependences: Powers of f (where $f = \sin\phi$; ϕ = latitude).

A: $f^{1/2}$, B: f^{0}, C: $f^{-1/2}$, D: f^{-1}.

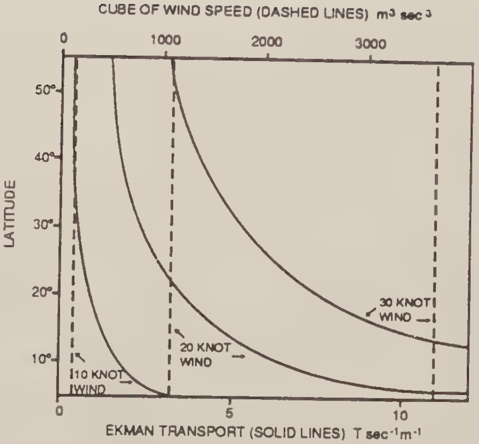

Figure 2. Turbulent mixing energy production (proportional to the third power of the wind speed), for several values of wind speed.

The optimal environmental window

Over the past several decades, empirical analyses of the relationships between local wind effects and recruitment variability in different eastern ocean pelagic fish populations have often yielded differing and, therefore, rather unsatisfying results (Bakun and Parrish 1980). Over the recent period of development of fishery-environmental science, reliance on linear statistics and empirical methods has been very much the fashion. Recently, effective nonlinear methods of empirical analysis have been introduced to fisheries science (Mendelssohn and Cury 1987; Mendelssohn and Mendo 1987). These methods were applied by Cury and Roy (1989) to the Peruvian anchoveta (*Engraulis ringens*), the California sardine (*Sardinops sagax caerulea*), the Moroccan sardine (*Sardina pilchardus*), and the Senegalese and Ivoirian sardinellas (*Sardinella aurita*). The result was a consistently domed-shaped relationship (Fig. 3, bottom) where reproductive success appeared highest at an intermediate wind strength which whether expressed as "W^3" rate of turbulent mixing energy input) or "$\mathcal{E}$" (wind stress, Ekman transport, upwelling index, etc.), consistently decomposed to a characteristic wind speed near 5 - 6 m s^{-1}. It is thus no mystery that the previous results may have been inconsistent. In cases in which most of the data may have been on the "left flank" (low wind speed side) of the optimal environmental window, an increasing relationship with wind speed would be found. Conversely, if most of the data were on the "right flank" (high wind speed side), a decreasing relationship with wind speed would be found. If the data were rather evenly distributed across both flanks of the window, linear methods could pick up no relationship at all.

Very recently, expansion of the analysis to additional stocks or data sets has yielded the same result. The California anchovy (*Engaulis mordax*) can be added to the list of "optimal environmental window" stocks (Roy *et al.* 1991). New recruitment estimates for the Moroccan sardine (Kifani 1991; Roy *et al.* 1991) and an analysis of pre-1945 data for the California sardine (Ware and Thomson, in press) showed the same characteristic "window" feature of maximum recruitment corresponding to an intermediate wind intensity during the larval period.

Constructing an interpretation of the optimal environmental window result is quite straightforward. It readily conforms to, and incorporates, the most prominent current hypotheses concerning variability in larval survival. The control on the "right flank", i.e., the "high wind" side, could come about either through (1) excessive offshore transport leading to offshore loss of pelagic larvae from the favorable coastal habitat (e.g. Parrish *et al.* 1981; Sinclair 1988) or through (2) overly intense turbulent mixing which could disperse fine-scale concentrations of appropriately sized and nutritious food particles needed for successful first feeding (Lasker 1975, 1978). An obvious explanation for the "left flank", or "low wind" side, is a lack of nutrient-enrichment by wind-induced upwelling or mixing, leading to inadequate production of appropriate larval food (Cushing 1969). Also, it is possible that under conditions where the interaction of feeding behavior with stable fine-scale food partical structure may be less important than the energy savings produced by turbulent diffusion of food particles toward feeding larvae, the mechanism of Rothschild and Osborn (1988) may exert some control on the "left flank" by increasing larval survival toward the slightly higher wind speeds within the "window".

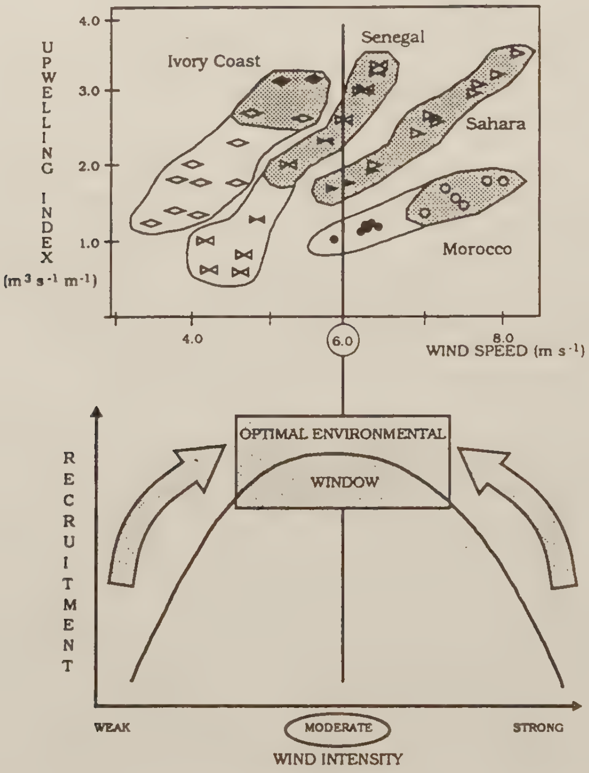

Figure 3 : Upper : annual monthly mean values of wind speed (m.s^{-1}) and upwelling indices (m^3.s^{-1}.m^{-1}) in the main West-African upwelling areas (Morocco, Sahara, Senegal and Ivory-Coast). A bold sign represents the months when reproduction is active and a shaded area represents the months when upwelling is active (from Roy et al., 1991).
Lower : theoretical relationship between recruitment and environmental factors in upwelling areas (from Cury and Roy, 1989).

Intriguing findings

Several intriguing findings invite explanation. The "optimal environmental window" appears to be remarkably stable among widely separated regions. It is nearly always centered very near an index value that, whether expressed as offshore Ekman transport or as turbulent mixing index, decomposes to a wind speed of about 6 m s^{-1} (Cury and Roy 1989, Roy *et al.* 1991). This seems to hold in upwelling systems located quite near the equator (Peru, Senegal), in mid-latitude upwelling ecosystems (California, Morocco), and at various points between (Op. cit.).

Another intriguing finding is the demonstration (Roy 1990; Roy *et al.*1991) of a striking difference in the seasonal relationship of peak reproductive activity to peak upwelling intensity between low latitude and mid-latitude habitats along the North Atlantic coast of Africa. In low latitude systems, the spawning peak tends to directly coincide with the period of maximum upwelling intensity. Conversely, in higher latitude systems, the peak spawning tends to be well before the seasonal upwelling peak, occurring in late winter to early spring. However, in both low and mid-latitude situations, the spawning peak does occur at a seasonal period typified by a mean wind speed very near the 6 m s^{-1} value (Fig. 3, upper panel) that consistently appears as the "optimal environmental window " in time series analysis.

A third intriguing finding, not particularly new but in fact a subject of conjecture for over two decades, is the apparently unique capacity of the Peru Current Ecosystem to support massive populations of coastal pelagic fishes. The anchoveta (*Engraulis ringens*) population of the Peru Current, was, prior to its collapse in the early 1970s, by far the largest neritic fish population ever recorded (e.g, Paulik, 1971). And in the subsequent period, the combined Peruvian and Chilean landings of sardine (*Sardinops sagax*) have reached the largest annual totals ever recorded for any eastern ocean sardine population. The intensity of the upwelling that occurs does not seem in itself to be the answer. On a year round basis, the intensity of the upwelling occuring off Peru appears to be no greater than that near Cap Blanc in the Canary Current system and to be substantially less than off Namibia (Lüderitz) in the Benguela system (Parrish *et al.*, 1983). What is it about the Peru Current ecosystem that makes it such a good place for giant populations of these fishes to develop?

Physical scales

In considering the balances of processes leading to the "optimal environmental window" and other attributes of favorable reproductive conditions, it is useful to specify significant horizontal and vertical physical scales. In deep waters, two different vertical scales appear to be of particular interest. One is the *mixed layer depth* (MLD). The MLD is the depth of the relatively homogeneous ocean surface layer above the seasonal thermocline. In general, even in the absence of active erosion of the thermocline by wind-generated turbulence, nocturnal cooling at the ocean surface would increase the surface water density enough to cause the waters within this mixed layer to be "turned over" at least once each day (otherwise, a discernable thermocline would build up, determining a new, shallower MLD). Thus larvae or other organisms that do not oppose this mixing by actively behaving so as to maintain themselves within a constant depth increment would tend, on average, to be rather evenly distributed over the MLD.

The second important vertical scale is the *Ekman depth*, $\mathcal{D}$. This is the depth to which significant wind-induced Ekman transport extends. An expression for the Ekman depth is (Ekman 1905):

$$\mathcal{D} = \pi\sqrt{\frac{2A_z}{\rho\ f}} \sim f^{-1/2} \qquad (2)$$

where A_z is the vertical eddy viscosity coefficient, and ρ is the density of sea water. $\mathcal{D}$ is generally thought to be of the order of 10 - 50 m, and probably does not extend significantly into stable density stratification. Thus, in general, $\mathcal{D} \leq$ MLD.

The offshore scale for dynamic ocean processes such as coastal upwelling is the Rossby radius of deformation, $\mathcal{R}$. We can thus think of $\mathcal{R}$ as the intrinsic scale for the coastal pelagic habitat. An expression for $\mathcal{R}$ applicable to coastal upwelling ecosystems is (Mooers and Allen 1973):

$$\mathcal{R} = \frac{HN}{f} \sim f^{-1} \qquad (3)$$

where H is the water depth and N is the Brunt-Vaisala frequency. Estimates of $\mathcal{R}$ are generally of the order of 10 - 20 km in mid-latitude eastern ocean coastal habitats. $\mathcal{R}$ obviously becomes much wider in tropical regions, due to the inverse dependence on f (curve "D", Fig. 1); eq. (3) becomes infinite at the equator itself.

A second dynamically-important offshore scale is the width of the continental shelf. The shelf width has been cited as being important for primary and secondary production (Binet 1991) and fish reproduction (Parrish *et al.* 1983; Nelson and Hutchings 1987). The upwelling region off Senegal provides an illustrative example. To the north of Cap Vert the continental shelf is rather narrow, sea surface temperature increases rather monotonically offshore and chlorophyll is rather uniform (Fig. 4, left panels). However, south of Cap Vert where the shelf abrubtly widens, the lowest sea surface temperature is not at the coast but over the continental shelf break (Fig. 4, left panels) and high phytoplankton biomass and productivity, indicated by clorophyll concentration (Fig 4) is apparently retained over the inner shelf (Gning *et al.* 1990), suggesting a double-celled upwelling circulation (Jacques and Tréguer 1986) which may provide an area of retention inshore of the most intense upwelling.

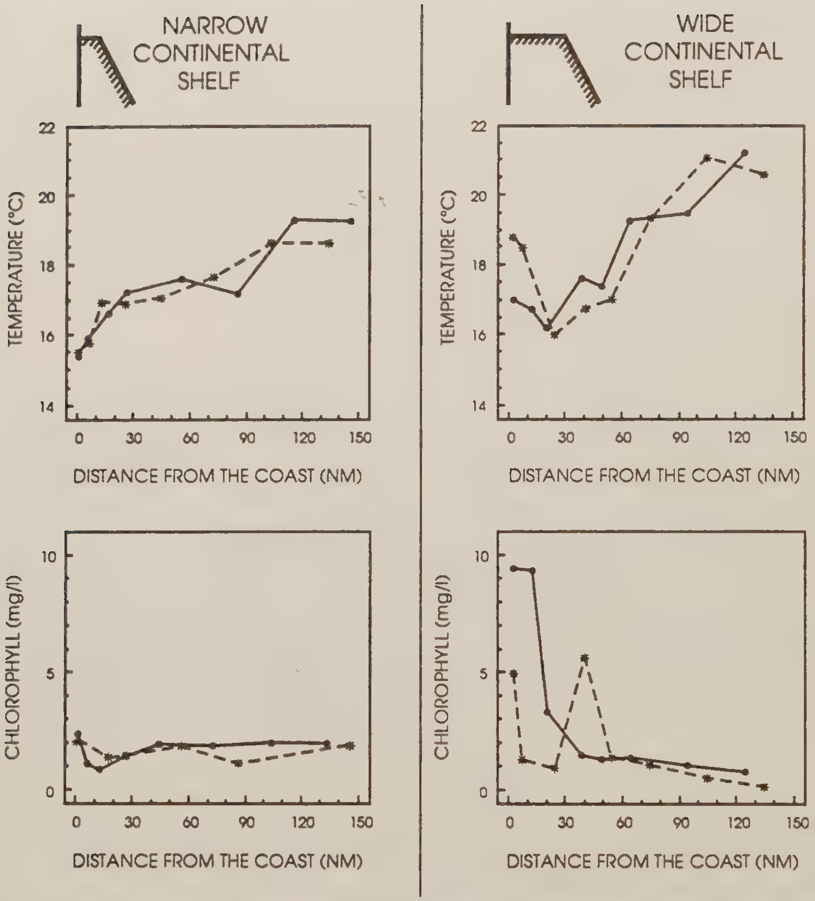

Figure 4 : Surface distribution of temperature (°C) (upper) and chlorophyll ($mg.l^{-1}$) (lower) along two transects off the Senegalese coast, for a narrow continental shelf (left) and a wide continental shelf (right),(from Gning et al., 1990).

Scaled offshore velocity

The Ekman volume transport of water can be approximated from an estimate of wind stress on the sea surface. However, it is not the magnitude of the transport (i.e., the number of m^3 per day per unit width of coastline) that determines the proportion of larvae that may be carried so far offshore that their chances of survival are severely impacted. Rather, it is the *speed* at which larvae are, on average, carried offshore that is the determining factor. This speed is determined by dividing the offshore volume transport by the appropriate depth scale to yield units of velocity (km day^{-1}, for example).

Further, the speed of offshore larval movement is only significant in relation to the offshore width of the favorable coastal habitat. For example, if the offshore habitat width is wider in one situation than in another, a greater offshore velocity may have less detrimental effect. To adjust for differences in habitat width, the speed can be divided by the appropriate offshore habitat scale. This finally yields what we will call the "scaled offshore (Ekman) velocity" or "SOV". Thus

$$\mathrm{SOV} = \frac{\mathcal{E}}{\text{depth scale} \times \text{offshore scale}} \qquad (4)$$

The SOV thus expresses, in relative terms, the fraction of the offshore habitat scale that is traversed per unit time by the "average" larvae due to offshore directed Ekman transport. We suggest SOV as the appropriate quantity for inter-regional or inter-seasonal comparisons of apparent effects of directly wind-driven offshore larval transport on reproductive success.

The qualification "in relative terms" is required in the previous paragraph because of uncertainties as to exact relationships of the physical scales to the "behavior-scales" of the organisms. This point may be illustrated by studying two different cases, each based on a different assumption concerning the manner in which active behavior of the organisms themselves might affect their depth distribution within the upper mixed layer of the ocean.

Case 1 (Fig. 5, upper panel) represents a case where a planktonic organism, such as larvae of a fish species, maintains its vertical position to remain within a shallow depth increment (not exceeding the Ekman depth) near the sea surface through active swimming behavior. In this case, the actual speed of offshore movement will depend on the details of the average vertical profile of Ekman velocity within the Ekman layer. These details are not well known or understood and are nearly impossible to measure, constituting large time and space averages of smaller-scale motions. However, for comparing different situations the Ekman depth, $\mathcal{E}$, may be the appropriate scale. This is because the speed of offshore movement should remain inversely proportional to the Ekman depth, assuming other factors are equal. For example, for a given rate of Ekman volume transport, a deeper Ekman layer will spread the depth distribution of Ekman velocity and cause each fixed depth increment to move at a slower speed. Thus for Case 1 (choosing the Rossby radius as the appropriate offshore habitat scale):

$$\text{SOV} = \frac{\mathcal{E}}{\mathcal{D} \times \mathcal{R}} = \frac{\sim f^{-1}}{\sim f^{-1/2} \times \sim f^{-1}} \sim f^{+1/2} \qquad (5)$$

Thus, for a given magnitude of wind stress, even though the Ekman transport increases toward the equator, under the assumptions of Case 1, the scaled offshore velocity (SOV) decreases toward the equator (curve "A", Fig. 1).

Case 2 (Fig. 5, lower panel) represents a case where the organisms exert no active control on their depth level within the mixed layer, but act approximately as neutrally-bouyant passive drifters. In such a case the organisms would, on average, be rather evenly distributed through the mixed layer. Here the depth of the Ekman layer is irrelevant, since the average offshore velocity of the mixed layer will be the total offshore volume transport of mixed layer water, regardless of its depth distribution within the mixed layer ($\mathcal{D} \leq$ MLD), divided by the depth of the mixed layer. Neutrally-bouyant passive drifters, mixed through the mixed layer, would experience the same average offshore velocity as the water particles within the mixed layer. Thus for Case 2:

$$\text{SOV} = \frac{\mathcal{E}}{\text{MLD} \times \mathcal{R}} = \frac{\sim f^{-1}}{\sim f^{0} \times \sim f^{-1}} \sim f^{0} \qquad (6)$$

In this case the SOV has no latitude dependence at all (curve "B", Fig. 1).

Presently there exists little basis for confidently choosing between Cases 1 and 2 (and other cases that might be constructed on the basis of slightly different assumptions). The primary purpose of most of the larval sampling of coastal pelagic fishes has been quantitative estimation of larval biomass, etc. Thus vertical structure in larval distributions has been regarded as an unwanted source of sampling variance. For this reason, sampling has often been designed with the intention of integrating such structure (e.g., by utilizing vertical or oblique net tows). As a result, we have relatively little information as to details of vertical larval distribution and behavior.

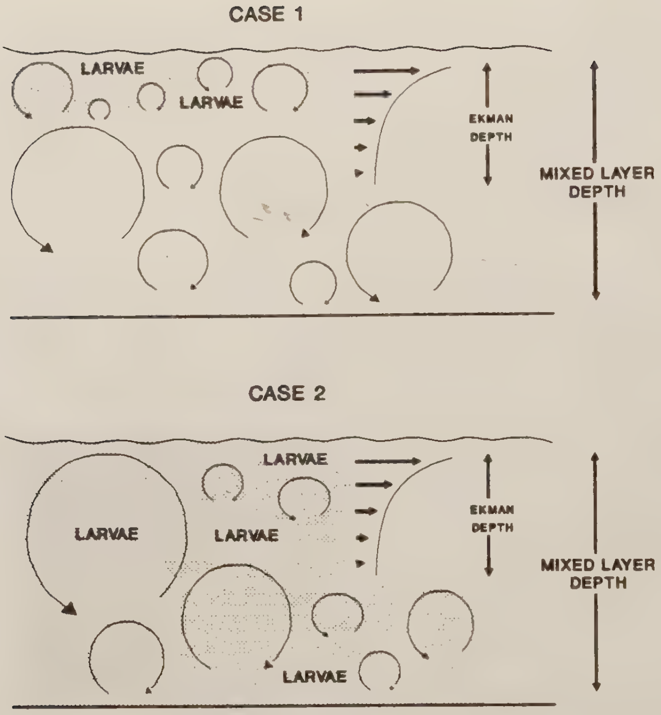

Figure 5. Schematic representations of the upper mixed layer of the ocean. The Ekman depth is represented by the exponentially-decreasing horizontal arrows. The depth of the larval distribution is represented by shading. Case 1: Larvae counter turbulent mixing and maintain their depth distribution within the upper Ekman layer by active behavior. Case 2: Larvae are passively mixed through the mixed layer.

Scaled enrichment factor

Nutrition-dependence of larval survival involves both avoidance of starvation and also the opportunity for rapid growth through the various size-dependent predation fields. Both starvation and growth depend on the energy balance between the caloric value of ingested food particles and the energy expended in locating and capturing those food particles. For small organisms such as larvae, the viscosity of sea water is substantial and active movement though it to find food exacts substantial energy costs. And each larva must strike that balance within the particular cubic meter of water in which it finds itself. Thus the nutrition-dependent component of larval survival rate depends not on the total quantity of appropriate food in the habitat but rather on its local concentration (quantity per unit habitat volume). Consequently, for the purpose of inter-regional or inter-seasonal comparisons of apparent effects of upwelling-based enrichment, the offshore Ekman transport (i.e., the upwelling index (Wooster and Reid 1963; Bakun 1973)) should be scaled according to the habitat volume by dividing $\mathcal{E}$ by the effective depth of larval habitat and by the offshore habitat scale. The larval habitat depth scale may be the MLD, as in "Case 2", above, or the behaviorally-maintained depth of larval incidence, as in "Case 1". Neither is a direct function of latitude. Thus if we choose the Rossby radius, $\mathcal{R}$, as the offshore scale, a "scaled enrichment factor" can be written:

$$\text{Scaled enrichment factor} = \frac{\mathcal{E}}{\text{larval depth scale} \times \mathcal{R}} = \frac{\sim f^{-1}}{\sim f^{0} \times \sim f^{-1}} \sim f^{0} \qquad (7)$$

i.e., a constant with respect to latitude (curve "B" in Fig. 1).

Discussion

With these concepts in hand, we now return to expand the discussion of the three intriguing findings pointed out earlier.

Latitudinal constancy of the "ideal" wind speed

The apparent constancy, over a range of latitudes, of the ideal wind intensity around which the the empirically-determined optimal environmental window (Cury and Roy 1989; Roy *et al.* 1991) is centered has seemed remarkable in view of the strong latitudinal dependences of some of the key processes and scales that are expected to be involved. However, if we apply proper scaling to the upwelling-based enrichment effect which is thought (Cury and Roy 1989) to be the primary mechanism controlling the low wind side of the "window", it may in fact be latitude-independent (eq. 7). Wind-generated turbulent mixing is not in itself latitude-dependent (Fig. 2). If turbulent mixing (Lasker 1975, 1978) controls the high wind side, a lack of latitude dependence in the "window" thus follows logically. In addition, a latitude-independent detrimental effect of offshore transport could also be involved on the high wind side of the "window" under the "Case 2" set of circumstances (larvae being rather haphazardly distributed mixed throughout the mixed layer and the Rossby radius being the appropriate offshore habitat scale) reflected in eq. 6.

Seasonal timing: spawning peak and upwelling peak -- in phase or out of phase?

Roy (1990) and Roy et al. (1991) report that in the low latitude systems off northwestern Africa, the spawning peak tends to directly coincide with the seasonal period of maximum upwelling intensity (Fréon 1988). Conversely, in the higher latitude coastal pelagic habitats of that region, the peak spawning tends to be well before the upwelling peak, occurring in late winter to early spring (Belvèze and Erzini 1983). However, in both low and mid-latitude situations, the spawning peak occurs within a seasonal period typified by a mean wind speed very near the 5 - 6 m s^{-1} value (Fig. 3, upper panel) that consistently appears as the "optimal environmental window" in time series analysis.

Since the observed spawning habits reflect the net adaptive response to a history of annual successes or failures in reproduction, one may not be surprised that spawning habits would be geographically and seasonally "tuned" to provide a successful match to the same optimal conditions that has apparently favored reproductive success in the set of recent years incorporated in the empirical time series analysis. We assume that upwelling-based nutrient enrichment of the local trophic system supports reproductive success. Thus the only reason for spawning to occur previous to a seasonal upwelling peak would be if upwelling turned out to have detrimental effects overbalancing the positive effects (e.g., increased offshore larval transport, destruction of stability and increased trubulent dispersion of food particle concentrations, changes of dominance from more nutritious flagellates to less nutritious diatoms, increased incidence of predators, etc.). With respect to offshore larval transport, we have shown that under certain likely sets of circumstances (e.g., "Case 1", discussed above) the SOV, which we have suggested as an appropriate interpretive measure of potential detrimental effects of offshore transport, decreases with decreased latitude (~ curve "A", in Fig. 1). Thus at lower latitudes, the stocks might be better able to experience the positive effects of spawning within a seasonal upwelling, while experiencing less negative effects from the associated offshore transport.

In the case of a different set of circumstances (e.g., "Case 2", discussed above) the SOV has no intrinsic latitudinal dependence. However, it is dependent on MLD (eq. 6) which may or may not have latitude dependence, but will probably have distinct seasonal dependence. For example, Parrish *et al.* (1983) note that the Peruvian anchoveta spawns during the winter upwelling peak. However, Bakun (1985) used the seasonal cycle of MLD, reported by Parrish *et al.* (1983), to show that the MLD deepened sufficiently during winter that the offshore velocity of the mixed layer was typically at a minimum during the upwelling peak. If fact, eq. (6) shows that when the seasonal cycle of MLD and $\mathcal{E}$ are in phase, in cases where the seasonal cycle of MLD has greater relative amplitude than that of $\mathcal{E}$, the seasonal cycles of $\mathcal{E}$ and SOV will be in opposite phase.

Here it is well to be reminded that other factors may also interact in determining optimal seasonal timing for peak reproductive effort. As seen in figure 4, high chlorophyll concentration exists along the Senegalese coast during the peak of the upwelling season. This implies a retention area where larvae could benefit from being kept near the coast within a highly productive area and season. Such a structure could explain the ability of fish to reproduce during the season of highest offshore transport. Roy (1990) has pointed out that the fish may solve the problem of offshore transport of their reproductive products by spawning habits which select locations for spawning where such physical retention mechanisms exist, leaving adjustment of seasonality as an available means for dealing with other factors (e.g., detrimental effects of turbulence).

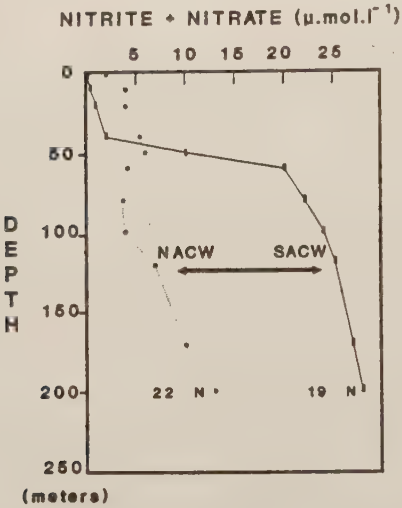

Figure 6 : Vertical profiles of nitrite and nitrate at 22N and 19N, showing the higher nutrient concentration of SACW compared to NACW, (adapted from Llinas *et al.*, 1985).

Also, part of the trade-off between positive effects of upwelling and negative effects of associated offshore transport involves qualitative aspects such as both the nutrient content of the upwelled water and the larval food value of the particular types of organisms that might utilize these nutients. For example, the North Atlantic Central Water acting as the primary upwelling source north of Cap Blanc (20° N) has a much lower NO_3 content than the South Atlantic Central Water to the south of Cap Blanc (Fig. 6); thus equal intensities of upwelling could result in greater actual upward nutrient transfer to the south of Cap Blanc than to the north.

A basis for the unique pelagic fish productivity of the Peru Current Ecosystem

The considerations presented herein perhaps shed some useful light on the remarkable capacity of the Peru Current Ecosystem to support particularly massive populations of coastal pelagic fishes. Since this habitat is located much nearer the equator than most of the other coastal upwelling habitats in which these fishes have been studied, the Rossby radius ($\mathcal{R}$), Ekman depth ($\mathcal{D}$) and Ekman transport ($\mathcal{E}$) all are large. Under the "Case 1" scenario, the SOV thus is small. And even if the"Case 2" scenario should be more apt, the MLD is very deep off Peru, during the winter spawning peak at least (Parrish *et al.* 1983), again yielding a relatively small SOV. The continental shelf width, which we discussed as an alternate scale for offshore extent of the coastal habitat, is also much wider off north-central Peru than in other eastern ocean coastal upwelling centers (see Table 6 in Parrish *et al.*,1983.). Turbulence generation by the wind is independent of f; and thus a given level of wind-driven offshore transport would tend to be accompanied by a much lower level of turbulence than in the other systems (Fig. 2). These considerations present a picture of a particularly benign environment off Peru where relatively weak winds result in strong offshore-directed surface Ekman transport (1.5 2.0 T s^{-1} m^{-1}) and an associated high volume rate of upwelling which continually enriches a very wide, deep, relative non-turbulent upper ocean habitat (i.e., mixing index values well within the 250 m^3 s^{-3} contour (Parrish *et al.*, 1983)). In the case of such a thick surface Ekman layer, the associated average offshore transport of larvae distributed through this layer would be relatively small, and their loss from a very wide coastal habitat would be minimized (i.e. a very low SOV). This same ease in maintaining standing stock in the upwelling-enriched environment and lack of exposure to intense turbulent mixing would be of similar benefit to primary producers, leading to high concentrations of food organisms for both larval and adult fishes. Note that as long as larval survival (per unit volume) is substantial, a large aggregate quantity of surviving larvae is favored by the latitude-dependent scaling factors which act to determine a very large total habitat volume per unit width of Peruvian coastline.

Concluding remarks

The considerations discussed in this paper are based on the class of "inferential approaches" (Anon. 1983), which includes comparative studies and analyses of interyear time series of temporally- and spatially-aggregated annual data points. Clearly, such approaches have only limited ability to sort out the types of interactions discussed above. Part of this limitation is due to the aggregation of energetic smaller-scale events into the annual temporal and spatial composites. This "smears together" separate causes and effects, that are determining the outcomes on the smaller scales, in a way that makes it very difficult to differentiate them by retrospective analysis. The problem of lack of resolution in our knowledge of processes and distributions in the vertical dimension, discussed above with respect to formulation of the SOV, is perhaps even more serious in the horizontal and temporal dimensions.

This is the reason that the operational approach within SARP is vital. High-resolution studies, both in time and space, are key elements of the SARP operational rationale (Bakun, Alheit, and Kullenberg, this session). The inferential and operational approaches should proceed together, continually feeding back and reinforcing one another. One of the purposes of this paper is to provide some conceptual framework and language that may help to integrate the two appoaches. The considerations presented in this paper may suggest certain key issues to the designers of operational field exercises. Certainly, one is the question of scale. We need to define the dominant scales, horizontal, vertical, and temporal, involved in the recruitment problem. Once better insight into these scales is available, the inferential process can proceed with much greater confidence and benefit.

Acknowledgements

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References

Anon. 1983. Workshop on the IREP Component of the IOC Programme on Ocean Science in Relation to Living Resources (OSLR). IOC Workshop Rep. 33. Intergovernmental Oceanographic Commission, Unesco, Paris. 51pp.

Bakun, A. (In press) The California Current, Benguela Current, and Southwestern Atlantic Shelf Ecosystems: A comparative approach to identifying factors regulating biomass yields. *In* Stress Mitigation and Preservation of Large Marine Ecosystems. K. Sherman, L. M. Alexander, and B. Gold (eds.). American Association for the Advancement of Science.

Bakun, A. 1973. Coastal upwelling indices, west coast of North America, 1946-71. NOAA Tech. Rep. NMFS SSRF-671. 103pp.

Bakun, A. 1985. Comparative studies and the recruitment problem: Searching for generalizations. CalCOFI Rep. 26: 30-40.

Bakun, A. 1990. Global climate change and intensification of coastal ocean upwelling. Science 247:198-201.

Bakun, A., Alheit, J., and Kullenberg, G. (this Symposium).The Sardine-Anchovy Recruitment Project (SARP): rationale, design and development. ICES-IOC Theme Session on "Results from the Sardine Anchovy Recruitment Project (SARP)", La Rochelle, France, 27 September 1991.

Bakun, A., and R.H. Parrish. 1980. Environmental inputs to fishery population models for eastern boundary current regions. pp. 67-104. In: G.D. Sharp (ed.) Workshop on the Effects of Environmental Variation on the survival of Larval Pelagic Fishes, Lima, Peru, 20 Apr.-5 May, 1980. IOC Workshop Rep. 28: 323pp.

Belvèze, H. and K. Erzini. 1983. The influence of hydroclimatic factors on the availability of the sardine (*Sardina pilchardus*, Walbaum) in the Moroccan Atlantic fishery. *In*: G.D. Sharp and J. Csirke (Ed.) Proceedings of the expert consultation to examine changes in abundance and species composition of neritic fish resources, FAO, Fish. Rep. 291 (2): 285-327.

Binet, D. 1991. Dynamique du plancton dans les eaux côtiètes ouest-africaines, écosystèmes équilibrés et déséquilibrés. In : Variabilité, instabilité et changement dans les pêcheries ouest africaines, P. Cury et C. Roy eds. ORSTOM, Paris.

Cury, P., and Roy, C. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. Can. J. Fish. Aquat. Sci. 46; 670-680.

Cushing, D.H. 1969. Upwelling and fish production. FAO Fish. Tech. Pap. 84. 40 pp.

Ekman, V. W. 1905. On the influence of the earth's rotation on ocean currents. Ark. Mat. Astron. Fys., 2(11): 1-55. (reprinted in J. Cons. int. Expl. Mer. 20(2), 1954.)

Fréon, P. 1988. Réponses et adaptations des stocks de clupéidés d'Afrique de l'ouest à la variabilité du milieu et de l'exploitation : Analyse et réflexion à partir de l'exemple du Sénégal. Etudes et Thèses, ORSTOM, 287 p.

Gning I., C. Roy et D. Toure, 1990. Variabilité spatio-temporelle de la temperature, des nitrates et de la chlorophylle devant les cotes du Sénégal. Doc. Sci. Cent. Rech. Oceanogr. Dakar-Thiaroye, 122, 21p.

Jacques, G. et P. Tréguer. 1986. Ecosystèmes pélagiques marins. Collection d'écologie, 19. Masson ed. Paris, 243p.

Kifani, S. 1991. Approaches spatio-temporelle des relations hydroclimat-dynamique des espèces pélagiques en région d'upwelling: cas de la sardine du stock central marocain. Thèse de Doctorat, Spécialité Océanographie halieutique. Univ. Bret. Occid. 290 pp.

Lasker, R. 1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull. U.S. 73: 453-462.

Lasker, R. 1978. The relation between oceanographic conditions and larval anchovy food in the California Current: Identification of the factors leading to recruitment failure. Rapp. P.-v. Reun. Cons. int. Explor. Mer. 173: 212-230.

Lasker, R. 1988. Studies on the northern anchovy; biology, recruitment, and fishery oceanography. p. 24-41 in: Studies on Fisheries Oceanography, Proceedings of the 25th Aniversary Symposium "Fisheries and Fishery Oceanography in the Coming Century". Tokyo, 10-13 Nov., 1986, Japanese Society of Fishery Oceanography.

Llinas, O., Fraga F. and E.D. Barton. 1985. Nutrient distributions in the central water mass front near Cabo Blanco, October 1981. In : C. Bas, R. Margalef and P. Rubies, eds. Simposio Internacional sobre las areas de afloramiento mas importantes del Oeste Africano. Intitudo de Investigaciones Pesqueras, Barcelona, Vol. 1, p. 37-48.

Mendelssohn, R. and Cury, P. 1987. Fluctuations of a fortnightly abundance index of the Ivoirian coastal pelagic species and associated environmental conditions. *Can. J. Fish. Aquat. Sci.* 44: 408-421.

Mendelssohn, R., and J. Mendo. 1987. Exploratory analysis of anchoveta recruitment off Peru and related environmental series. p. 294-306. In: D. Pauly and I. Tsukayama (eds.) The Peruvian Anchoveta and Its Upwelling Ecosystem: Three Decades of Change. *ICLARM Studies and Reviews* 15.

Mooers, C. and Allen, J.S. 1973. Final Report of the Coastal Upwelling Ecosystems Analysis Summer 1973 Theoretical Workshop. School of Oceanography, Oregon State University, Corvallis, Oregon. 137 pp.

Nelson, G and L. Hutchings, 1987. Passive transportation of pelagic system components in the Southern Benguela area. In : Payne, A.I.L., Gulland J.A. and K.H. Brink, (eds.), the Benguela and comparative ecosystems. S. Afr. J mar. Sci., 5: 223-234.

Parrish, R.H., A. Bakun, D.M. Husby, and C.S. Nelson. 1983. Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish reproduction. *In* Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources. pp. 731-778. Ed. by G.D. Sharp and J. Csirke. FAO Fish. Rep. 291. 1224 pp.

Parrish, R.H., Nelson, C.S., and Bakun, A. 1981. Transport mechanisms and reproductive success of fishes in the California Current. Biol. Oceanogr., 1: 175-203.

Paulik, G.J. 1971. Anchovies, birds, and fisherimen in the Peru Current.*In* Environment, Resources, Pollution and Society. pp. 156-185 Ed. by W.W. Murdock. Sinauer Press, Stamford, Conn.

Peterman, R.M., and Bradford, M.J. 1987. Wind speed and mortality rate of a marine fish, the northern anchovy (*Engraulis mordax*). Science 235: 354-356.

Rothschild, B.J. and Osborn, T.R. 1988. Small-scale turbulence and plankton contact rates. J. Plankton Res. 10: 465-474.

Roy, C. 1990. Réponses des stocks de poissons pélagiques à la dynamique des upwellings en Afrique de l'Ouest: analyse et modélisation. Thèse de Doctorat. Université de Bretagne Occidental, Brest, France.147 pp.

Roy, C., Cury, P., and Kifani, S. 1991. Optimal environmental window and pelagic fish reproductive strategies in upwelling areas. International Symposium on Benguela Trophic Functioning, Resource Utilization from an Ecosystem Perspective, Cape Town, South Africa, 8-13 Sep 1991.

Shepard, J.G., Pope, J.G., and Cousins, R.D. 1984. Variations in fish stocks and hypotheses concerning their links with climate. Rapp. P.-v. Reun. Cons. int. Explor. Mer 185: 255-267.

Sinclair, M. 1988. Marine Populations: an essay on population regulation and speciation. University of Washington Sea Grant Program (Distributed by University of Washington Press. Seattle and London.) 252 pp.

Ware, D. M., and Thomson, R. E. (in press) Link between long-term variability and fish production in the northeast Pacific Ocean. Can. J. Fish. Aquat. Sci. 48.

Wooster, W. S., and J. L. Reid, Jr., 1963: Eastern boundary currents. *The Sea*, Vol. 2, M. N. Hill, Ed., Wiley Interscience, 253-280.

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Marine Turtle Newsletter

SEA TURTLE TAG CENTER OF THE PACIFIC

The Sea Turtle Tag Center of the Pacific is a cooperative program to make available tags, tag applicators, and technical assistance in the tagging of sea turtles for research purposes to government and other qualified organizations in the Pacific islands region of Polynesia, Micronesia, and Melanesia. The program is jointly conducted by the Southwest Fisheries Center Honolulu Laboratory of the National Marine Fisheries Service, and the University of Hawaii's Hawaii Institute of Marine Biology (HIMB). The program is designed in particular to aid those locations where small to moderate numbers of tags (i.e., 100-500) are needed, and local authorities or organizations might not otherwise order them from the manufacturer.

The tags available for use are made of Inconel, a superior corrosion-resistant alloy composed of cadmium and nickel. The tags are self-piercing, self-locking, and simple to use when applied with a special plier-like applicator to the trailing edge of a turtle's front flippers. All tags are imprinted consecutively with a letter-number combination to identify individual turtles. In addition, the following inscription appears on each tag:

Write HIMB
University
Hawaii 96744

Persons who report the sighting of a tagged turtle to this address are sent a T-shirt bearing a sea turtle logo. The sighting information that is received is relayed in a timely manner to the research organization responsible for tagging the turtle. The distribution of tags in the Pacific region under this cooperative program has been underway for several years, but without the benefit of a formal name until now. Organizations interested in receiving more information about the availability of tags from the Sea Turtle Tag Center of the Pacific should write to George Balazs at the address below.

GEORGE H. BALAZS, NMFS Southwest Fisheries Center Honolulu Laboratory, 2570 Dole Street, Honolulu, Hawaii 96822-2396 USA [FAX: (808) 942-2062].

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The Utility of Demographic Models in Marine Mammal Management

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ABSTRACT

Demographic models can be used to estimate population growth rate directly from the stable distributions of age and reproductive state. Two demographic models are considered: the geometric series and Leslie matrix models. Both models are shown to converge to the same estimator for population growth rate, e^r. A method is derived which estimates the sampling variance in e^r using this estimator. The variance of this estimator is calculated for three examples of marine mammal life history and for sample sizes ranging from 500 to 16,000. Even with the largest sample sizes and ignoring numerous sources of additional variability, the sampling variance in estimates of population growth rate is too large to be of practical value in marine mammal management.

INTRODUCTION

Demographic models are used to represent the dynamics of age-structured populations. They can range in complexity from simple 2-age models which consider only 'juveniles' and 'adults', to full Leslie matrix models which typically include one age class for each year of life. Demographic models have had a long history of use in the management of marine mammal populations (Allen, 1981).

Although demographic models have many uses, the most misunderstood (and perhaps the most emphasized) has been the estimation of population growth rates. In this paper I examine this particular use in detail and evaluate whether such models can provide estimates of population growth rates that are useful in the context of marine mammal management.

Several previous studies have investigated the accuracy with which growth rates can be estimated from measurement of demographic parameters. Lenski and Service (1982) and Meyer *et al.* (1986) derive variance estimators based on data that are gathered from a longitudinal study of a cohort. These data, however, are not available for marine mammals. For large whales, the emphasis has been on the accuracy of estimating natural mortality rates from catch-at-age data with independently measured trends in abundance (Tanaka, 1990). De la Mare (1990a) has shown that mortality rates estimated by these methods are not precise. In a more general sensitivity study, de la Mare (1990b) has shown that net recruitment rates are very sensitive to errors in estimating demographic parameters. Here I examine the sampling variance in estimating population growth rates from demographic parameters alone, independent of any information on trends in abundance.

DEMOGRAPHIC MODELS

In this paper I will consider two common demographic models which represent opposite extremes on a spectrum from simple to complex. These models are the geometric series model and the Leslie matrix model (respectively). As is common practice for both models, I will explicitly consider only the female segment of the population.

The geometric series model describes the most basic elements of age structure with only four parameters: the mean survival rate of reproductive females (p), the mean birth rate of reproductive females (m), the age at sexual maturation (α) and the survivorship from birth to the age of sexual maturity (l_α). Given these four parameters, population growth rate (e^r) can be estimated by solving its characteristic equation:

$$1 = (m\ l_\alpha)/(e^{r\alpha} - pe^{r(\alpha-1)}) \tag{1}$$

Goodman (1984).

The Leslie matrix model typically has many more parameters than the geometric series model. For marine mammals, this model will usually have two parameters (age-specific birth and death rates) for each year of life up to the maximum age attained by the species. This level of resolution has been chosen because it is typical of the level of resolution in age estimation for marine mammals. I use the terminology of Caswell (1989) for a birth-pulse population with postbreeding census. Age-specific survival rates (P_x) form the first sub-diagonal of the matrix and represent the probability of surviving from age class x to age class $x+1$. Age-specific fecundity rates (F_x) form the first row of the matrix and represent the expected number of female offspring born to a female in age class x at time t and which are alive at time $t+1$. Although the population growth rate (e^r) can be estimated by using linear algebra to find the dominant eigen value of the Leslie matrix, it is mathematically equivalent and algebraically simpler to solve the following characteristic equation:

$$1 = \sum_{i=1}^{\beta} e^{-rx} \cdot \mathrm{l}_x \cdot \mathrm{F}_x \tag{2}$$

where $\quad l_x = \prod_{i=1}^{x-1} p_i$

and $\quad \beta$ = maximum age class.

ESTIMATING DEMOGRAPHIC PARAMETERS

Given age-specific fecundity and survival rates, the estimation of population growth rates using demographic models is a simple algebraic exercise. The real problem is in accurately estimating the birth and survival parameters.

Survival rates can be estimated from the age distribution of a population if a number of assumptions are met. The primary assumption is that the population is in a stable age distribution. Although a method has been developed which circumvents this assumption (Fryxell, 1986), this method requires knowledge of both the actual, time-dependent age distribution and the distribution of ages at death. The latter is not available for marine mammal populations. Given a stable age distribution, survival rates can only be estimated as an 'apparent survival rate' (i.e. the true survival rate divided by the population growth rate). As pointed out by Caughley (1966), true survival rates can be estimated from age-frequency distributions alone only if the population is not growing. Fortunately, it has been shown for the Leslie (Michod and Anderson, 1980) and geometric series (Goodman, 1984) models, that knowledge of the 'apparent survival rate' is sufficient to estimate population growth rate using either model. Although many smoothing models have been proposed for the estimation of the age-specific survival rate, these complications are not necessary when estimating the population growth rate. As will be shown below for both the geometric series and Leslie models, the only relevant survival statistic is the ratio of the number of individuals in reproductive age classes to the number of individuals in the first age class.

Estimating the fecundity parameter(s) of either model is more complicated than simply measuring crude birth rates. In both models, the fecundity term incorporates elements of survival of the mother from census to birth and/or the offspring from birth to census. Methods of estimating Leslie-matrix fecundities (F_x) from field data are discussed by Goodman (1984) and Caswell (1989). The fecundity term in the geometric series model (m) is a weighted average of the age-specific fecundities of the reproductive age classes where the weights are given by the stable age distribution (Goodman, 1984). If the population is in stable age distribution (which is a necessary condition for estimating population growth rates) m can be estimated from a random sample of reproductive females and the appropriate weighting will be implicit.

ESTIMATING POPULATION GROWTH RATES

Substituting the 'apparent survival rate' (i.e. the true rate divided by the population growth rate) in Equations 1 and 2 results in considerable simplification; both can then be represented as direct solutions for e^r.

Geometric Series Model

The characteristic equation for the geometric series model (Eq. 1) simplifies to:

$$e^r = (m\, l'_\alpha)/(1 - p') \qquad (3)$$

where p' = the apparent survival rate

and l'_α = the apparent survivorship to age α

(incorrectly printed as Eq. 33 in Goodman (1984)). The apparent survival rate can be estimated as

$$p' = 1 - (n_{\alpha+}/N) \qquad (4)$$

where $n_{\alpha+}$ = the number in reproductive age classes,

and N = the total number in all age classes

(Goodman (1984), from his Eq. 24). The apparent survivorship to age α can be estimated as

$$l'_\alpha = n_{\alpha+}/n_1 \qquad (5)$$

where n_1 = the number in age class 1

(Goodman (1984), from his Eq. 32). Substituting Equations 4 and 5 into 3, population growth rate can thus be represented as

$$e^r = (m\, n_{\alpha+})/n_1 \qquad (6)$$

The numerator in Equation 6 represents the number of offspring that will be produced by females at time t and which will survive until census at time $t+1$. Assuming that gestation is one year and ignoring the survival aspect of fecundity, the fecundity rate, m, can be estimated as the number of pregnant females, n_p, divided by the total number of mature females, $n_{\alpha+}$. Thus Equation 6 can be re-expressed as

$$e^r = n_p/n_1 \qquad (7)$$

Leslie Matrix Model

A similar simplification is possible with the characteristic equation for the Leslie matrix (Eq. 2). Again, population growth rate can be expressed in terms of age-class abundances and fecundity

$$e^r = \frac{\sum_{x=\alpha}^{\beta} F_x \cdot n_x}{n_1} \qquad (8)$$

(Michod and Anderson (1980), from their Eq. 3). The similarity between Equations 6 and 8 is more than superficial.

The numerator in both represents the number of offspring that will be produced by mature females at time t and which will survive until census at time $t+1$. Again assuming that gestation is one year and ignoring the survival aspect of fecundity, Equation 8 can be reduced to Equation 7. The estimation of population growth rates for both the geometric series and Leslie matrix models has thus converged on a single approach.

The data which will be needed to estimate population growth rate will thus be the number of pregnant females and the number of individuals in the first age class.

VARIANCE ESTIMATION

The estimation of population growth rate has been reduced to the ratio of two elements of a multinomial distribution. This makes the problem of estimating its variance simple. Let q_1 be the expected proportion in age class 1 in the population, let q_p be the expected proportion of pregnant females, and let N be sample size of all age and reproductive classes. The sampling variance in e^r can be estimated from the Taylor series approximation for the variance of a ratio (Yates, 1953) using multinomial variance and covariance estimators. Thus

$$var(e^r) = var\left[\frac{n_p}{n_1}\right] = \left[\frac{{q_p}^2}{q_1}\right] \cdot \left[\frac{1-q_p}{N\cdot q_p} + \frac{1-q_1}{N\cdot q_1} + \frac{2}{N}\right] \qquad (9)$$

For simplicity I have glossed-over all the complications involved in estimating fecundity from data on gross percent pregnant. As stated previously, fecundity includes an element of survival. I have assumed that this survival rate is 1.0. The survival part of the fecundity term is typically very difficult to measure and its estimation will add to the sampling variance associated with estimating population growth rates. Furthermore, I have assumed that age and reproductive status can be measured without error. For these reasons the variance estimated here will underestimate the true variance expected from any real sampling plan.

MONTE CARLO SIMULATIONS

A simple simulation is used to test Equation 9 and to examine the distribution of estimated population growth rates. I assume that the population can be sampled randomly with respect to age and reproductive condition. I draw random samples from a hypothetical population of females and record (1) the number in the first age class and (2) the number of pregnant females. For each sample, population growth rates are estimated from Equation 7. Thus, in this simulation I assume that all errors in estimating population growth result from random sampling of a multinomial distribution.

The expected fraction of the female population in each of the two categories given above is dependent on both the age-specific fecundities and survival rates. Consequently, the simulations require some assumptions about the life history of the species. Three model life tables will be used as representative examples in the simulation. Case I is a generalized marine mammal with an adult survival rate of 0.9, a mean adult fecundity rate of 0.21, an age of sexual maturity of 6 years, a survivorship from birth to sexual maturity of 0.506 and a population growth rate of 1.000. Case II is the same generalized marine mammal except with a mean fecundity of 0.45 and a population growth rate of 1.065. Case III is modeled specifically after the spotted dolphin (*Stenella attenuata*) with age specific fecundity and survivorship as illustrated in Fig. 1 and with a population growth rate of 1.024. The expected frequency of individuals in the first age class, all other immature age classes, the mature pregnant and the mature not-pregnant groups are given in Table 1 for each of the three examples.

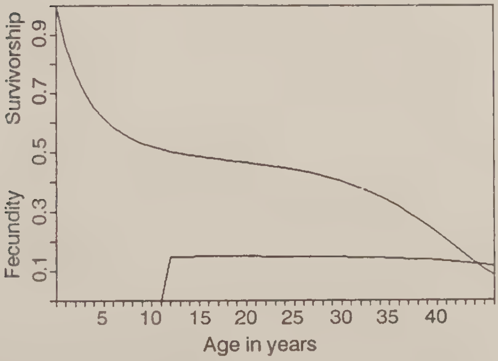

Fig. 1. Age-specific survivorship and fecundity rates used to model the spotted dolphin (from Barlow and Boveng 1991) in Case III of the simulation study.

To simulate sampling from a real population, samples were drawn randomly from the multinomial distributions given in Table 1. Samples sizes of 500, 1,000, 2,000, 4,000, 8,000 and 16,000 females were drawn for each of the three sample life tables. Population growth rates were calculated from each sample, and sampling was repeated 1,000 times to estimate the mean and variance of the estimated population growth rates.

RESULTS

The distributions of estimated population growth rates from the simulations are given in Figs 2 to 4 for the three life table examples (all based on a sample size of 4,000 females). In all three cases, the mean growth rate is in reasonable agreement with the expected mean growth rate, but the range of estimated growth rates is wide and appears skewed. Mean and standard deviations of population growth rates are given in Table 2. Estimates of standard deviation based on Equation 9 are generally in good agreement with the simulation results, but for smaller sample sizes, growth rates and standard deviations are consistently lower than for the simulation (possibly linked to the truncation of third and higher-order terms in

Table 1

Expected proportion of females that are in each of four age-reproductive classes (in year class 1, in other immature age classes, pregnant with a female fetus, and mature but not pregnant with a female fetus) for a population in stable age distribution.

Life table example	Age class one	Other immature ages	Mature and pregnant	Mature not pregnant
Case I	0.118	0.313	0.118	0.451
Case II	0.177	0.404	0.188	0.230
Case III	0.072	0.430	0.074	0.424

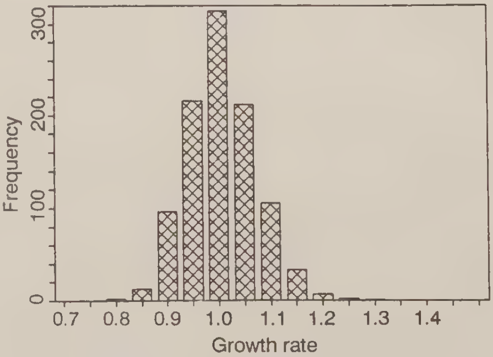

Fig. 2. Frequency distribution of estimated population growth rates for Case I based on 1,000 samples of 4,000 females.

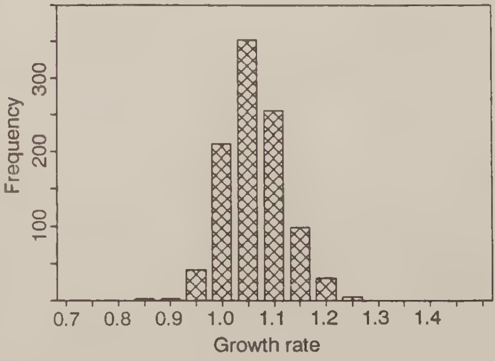

Fig. 3. Frequency distribution of estimated population growth rates for Case II based on 1,000 samples of 4,000 females.

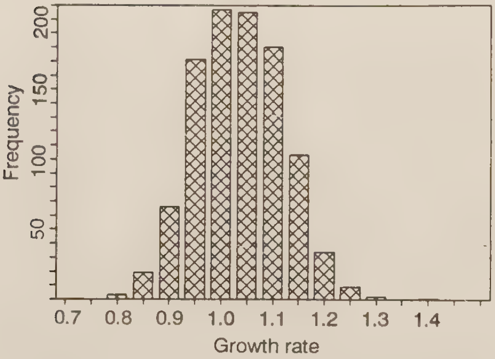

Fig. 4. Frequency distribution of estimated population growth rates for Case III based on 1,000 samples of 4,000 females.

Table 2

Standard deviations of growth rates estimated from Equation 9 and from Monte Carlo simulation. Simulation results are based on 1,000 replicates of the given sample size.

Life table example	Sample size	Analytical growth rate	Standard deviation	Bootstrap growth rate	Standard deviation
Case I	500	1.000	0.184	1.029	0.193
	1000	1.000	0.130	1.012	0.137
	2000	1.000	0.092	1.004	0.095
	4000	1.000	0.065	1.005	0.067
Case II	500	1.065	0.157	1.073	0.163
	1000	1.065	0.111	1.060	0.109
	2000	1.065	0.079	1.059	0.079
	4000	1.065	0.056	1.064	0.056
Case III	500	1.024	0.241	1.059	0.258
	1000	1.024	0.170	1.042	0.177
	2000	1.024	0.120	1.031	0.123
	4000	1.024	0.085	1.035	0.084

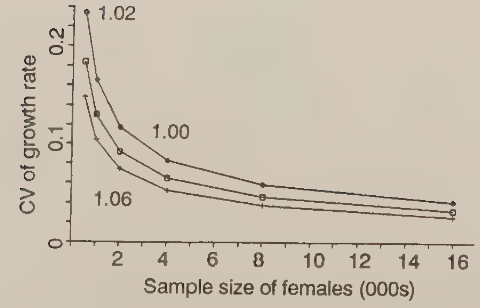

Fig. 5. Analytically derived estimates of the coefficients of variation in population growth rates as a function of sample size for each of the 3 cases used in the simulation. From top to bottom, Cases III, I, and II.

deriving Equation 9). Coefficients of variation in annual growth rate, e^r, are illustrated as functions of sample size in Fig. 5.

DISCUSSION

Results indicate that even under the most optimistic scenario, extremely large sample sizes are required to accurately estimate population growth rates. Even with a sample size of 4,000 females, biologically implausibly high growth rates were frequently estimated. These results were based on the assumption that random sampling was the only source of error. Many other important sources of variation were ignored. If those other sources of variation were included, the situation could only be worse. It is unlikely that unbiased samples could be collected from a sufficient number of individuals for this approach to be useful in managing marine mammal populations.

Although coefficients of variation of less than 10% are typically considered good in ecological studies, values less than 1% are probably necessary for estimates of population growth to be useful in the management of harvests. The reason for this is that it is the annual increment (e^r-1), not e^r, that is of interest in determining harvest rates. When population growth is small, a CV of 1% in e^r can be equivalent to a CV of 100% in e^r-1. This level of accuracy would provide little useful information and clearly should not be used as a sole basis for determining acceptable harvest rates.

The sample sizes required to estimate population growth rates to within 1% were outside the range of values that I considered. It is easy to see from Fig. 5 that the required sample would be much greater than 16,000 females. There are many practical reasons why such large samples may be unobtainable. It should be remembered that in taking such a sample, it is likely that an equal number of males would have to be caught and examined (i.e. a total sample of much greater than 30,000 animals). The cost of obtaining such a large sample using unbiased collection methods would be staggering. Furthermore, the method is very sensitive to the ratio of reproductive females to females in year-class 1. Because juveniles usually segregate from adults, an unbiased estimate of this ratio may not be obtainable at any cost.

Although based on Fig. 5, the utility of demographic estimates of population growth rate already looks dismal, it is important to consider the sources of variation that were ignored in the simulation. Perhaps the biggest source of error will come from biases in sampling. In previous attempts at obtaining unbiased samples of minke whale populations, Kishino *et al.* (1989) found that different age groups segregated into different characteristic group sizes and in different geographic areas. Random sampling of groups of different size is difficult because the ability to find groups varies with group size. Correction for the geographic segregation of age groups is difficult because it requires knowledge of the density of animals in each geographic stratum. Assuming that all these potential biases can be corrected, the correction process itself will introduce an additional source of sampling variance. Errors in the estimation of age and reproductive status are unavoidable. Assuming that this type of error can be measured, correction will again add additional sources of variation. Yet another problem is that populations may not be in stable age distribution. A long time series of samples would be required just to determine if this important assumption has been met.

The direct estimation of population growth rate is not the only use of demographic models. Demographic models have already been useful in estimating the upper limits on population growth of marine mammals (Reilly and Barlow, 1986; Barlow and Boveng, 1991). Also, the method of using stable age distributions is not the only method of estimating demographic parameters. Buckland (1990) and Barlow (1990) investigate alternative methods based on longitudinal studies of individually identifiable whales. The point of this study is not to denigrate the general value of demographic data. My main point is that one should have realistic ideas about what sample sizes are needed to estimate population growth rates using demographic models. Seldom, however, have the sample size requirements of demographic models for any purpose been tested **before** researchers go out and start collecting data. Data are collected in the optimistic anticipation that they will be useful when plugged into a demographic model. Often a simulation study such as the one presented here would have revealed the task was hopeless with any reasonable sample size. Tremendous expense could be saved, and we would not deceive ourselves into thinking that we were collecting all the information needed to make intelligent management decisions. Proper experimental design with a full analysis of all potential sources of error should be standard procedure before embarking on any large-scale research project.

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REFERENCES

Allen, K.R. 1981. Application of population models to large whales. pp. 263–75. *In:* C.W. Fowler and T.D. Smith (eds.) *Dynamics of Large Mammal Populations*. Wiley and Sons, New York. xviii+477pp.

Barlow, J. 1990. A birth-interval model for estimating cetacean reproductive rates from resighting data. *Rep. int. Whal. Commn* (special issue 12):155–60.

Barlow, J. and Boveng, P. 1991. Modelling age-specific mortality for marine mammal populations. *Mar. Mammal Sci.* 7(1):84–119.

Buckland, S.T. 1990. Estimation of survival rates from sightings of individually identifiable whales. *Rep. int. Whal. Commn* (special issue 12):149–53.

Caswell, H. 1989. *Matrix Population Models: Construction, Analysis and Interpretation*. Sinauer Associates, Sunderland, Massachusetts. 328pp.

Caughley, G. 1966. Mortality patterns in mammals. *Ecology* 47:906–18..

de la Mare, W.K. 1990a. A further note on the simultaneous estimation of natural mortality rate and population trend from catch-at-age-data. *Rep. int. Whal. Commn* 40:489–92.

de la Mare, W.K. 1990b. Inferring net recruitment rates from changes in demographic parameters: a sensitivity analysis. *Rep. int. Whal. Commn* 40:525–9.

Fryxell, J.M. 1986. Age-specific mortality: an alternative approach. *Ecology* 67(7):1687–92.

Goodman, D. 1984. Statistics of reproductive rate estimates, and their implication for population projection. *Rep. int. Whal. Commn* (special issue 6):161–73.

Kishino, H., Kato, H., Kasamatsu, F. and Fujise, Y. 1989. Statistical method for the estimation of age composition and biological parameters of the population. Paper SC/41/SHMi3 presented to the IWC Scientific Committee, May 1989 (unpublished).

Lenski, R.E. and Service, P.M. 1982. The statistical analysis of population growth rates calculated from schedules of survivorship and fecundity. *Ecology* 63(3):655–62.

Meyer, J.S., Ingersoll, C.G., McDonald, L.L. and Boyce, M.S. 1986. Estimating uncertainty in population growth rates: jackknife vs. bootstrap techniques. *Ecology* 67(5):1156–66.

Michod, R.A. and Anderson, W.W. 1980. On calculating demographic parameters from age frequency data. *Ecology* 61:265–9.

Reilly, S.B. and Barlow, J. 1986. Rates of increase in dolphin population size. *Fish. Bull., US* 84(3):527–33.

Tanaka, S. 1990. Estimation of natural mortality coefficient of whales from the estimates of abundance and age composition data obtained from research catches. *Rep. int. Whal. Commn* 40:531–6.

Yates, F. 1953. *Sampling Methods for Censuses and Surveys*. Hafner Publishing Co. Inc., New York. 401pp.

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MODELING AGE-SPECIFIC MORTALITY FOR MARINE MAMMAL POPULATIONS

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ABSTRACT

A method is presented for estimating age-specific mortality based on minimal information: a model life table and an estimate of longevity. This approach uses expected patterns of mammalian survivorship to define a general model of age-specific mortality rates. One such model life table is based on data for northern fur seals (*Callorhinus ursinus*) using Siler's (1979) 5-parameter competing risk model. Alternative model life tables are based on historical data for human females and on a published model for Old World monkeys. Survival rates for a marine mammal species are then calculated by scaling these models by the longevity of that species. By using a realistic model (instead of assuming constant mortality), one can see more easily the real biological limits to population growth. The mortality estimation procedure is illustrated with examples of spotted dolphins (*Stenella attenuata*) and harbor porpoise (*Phocoena phocoena*).

Key words: mortality estimation, longevity, survival rates, Leslie matrix, demography, *Callorhinus, Phocoena, Stenella.*

Demographic models are commonly used to study the dynamics of marine mammal populations. Such models are characterized by an explicit representation of age structure. This is desirable for animals, such as marine mammals, which have delayed maturation, long life spans, and for which aging methods are well established. The primary building blocks for demographic models are age-specific birth rates and survival rates.

Of these, age-specific survival rates have been generally more difficult to estimate. Several methods have been used to estimate survival (or mortality) rates from age-frequency distributions. All of these methods depend critically on the assumption that a population is in stable age distribution and is not growing (or, if growing, it is assumed that the rate of growth is constant and is known) (Caughley 1966, 1977). This, of course, limits the usefulness of demographic models for estimating the growth rate of a population. Such models are still useful in defining ranges of possible growth rates (Eberhardt 1985, Reilly and Barlow 1986), in establishing rational harvesting strategies (Goodman 1978), or in determining the optimal age structure to promote rapid recovery of a population (Goodman 1980).

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Typically, mortality has been estimated as a constant rate across many (or all) age classes. In fact, the pattern of mortality over a typical mammalian life span consists of an initial period of high juvenile mortality, followed by a period of relatively low mortality, and concluding with a period of rapidly increasing senescent mortality (Caughley 1966, Spinage 1972, Siler 1979). In the few instances for which sufficient data are available, marine mammals follow the same pattern (Chapman 1964, de la Mare 1986). Several mortality models have been proposed to fit age-frequency distributions for populations with this pattern (Caughley 1966, Siler 1979, Paranjpe and Rajarshi 1986).

Although survival or mortality rates can be estimated by fitting non-linear survivorship models to age-frequency distributions, there are problems in applying this approach for most populations. Often a population is not in a stable age distribution, or if it is, the age distribution cannot be determined without bias. It is difficult to obtain the large sample sizes that are needed to estimate mortality rates accurately. One or more age classes in a population are often missing or are underrepresented in the sample.

For human demographers, one solution to these problems has been to use model life tables (Gage 1988). A life table based on a population with good data is used to smooth, to interpolate missing values, or simply as a surrogate for the life table of another population with insufficient data. This approach has recently been extended to modeling mortality for Old World monkeys as well (Gage and Dyke 1988). In general, model life tables based on mathematical models (such as Siler's model) are now preferred over the older tabular approach (Gage 1988). For humans, Siler's 5-parameter model has been shown to give better fits than an alternative 4-parameter logit model (Gage and Dyke 1986).

In this paper, we present a simple method of estimating mortality rates based on minimal information: a model life table and an estimate of the longevity of the species. We demonstrate the utility of our approach using data from three marine mammal populations. Age-specific mortality rates are estimated for northern fur seals (*Callorhinus ursinus*). This model is used with two other model life tables (a population of human females circa 1900 and Old World monkeys) to estimate survival rates of other species. The first example, spotted dolphins (*Stenella attenuata*), is used to illustrate how our approach can be used to estimate ranges in current population growth rate given relatively detailed reproductive information and sparse mortality data. The second example, harbor propoise (*Phocoena phocoena*), is used to illustrate how limits can be placed on the maximum possible growth rate given minimal information on mortality and fecundity.

METHODS

Constructing a survivorship model—Siler's competing risk model (Siler 1979) was used as the basis for constructing a general model of survivorship for marine mammals. In this model, the total risk of mortality at a given age is the sum of an exponentially decreasing risk due to juvenile mortality factors, an exponentially increasing risk due to senescent mortality factors, and a constant risk due to other factors. In this model, the probability of survivorship from birth to age x can be expressed as:

$$l(x) = l_j(x) \cdot l_c(x) \cdot l_s(x), \tag{1}$$

where

$$l_j(x) = \exp[(-a_1/b_1) \cdot \{1 - \exp(-b_1 \cdot x/\Omega)\}], \tag{2}$$

$$l_c(x) = \exp[-a_2 \cdot x/\Omega], \tag{3}$$

and

$$l_s(x) = \exp[(a_3/b_3) \cdot \{1 - \exp(b_3 \cdot x/\Omega)\}]. \tag{4}$$

The survivorship l_c (Eq. 3) represents the constant risk of mortality experienced by all age classes. The survivorships l_j and l_s (Eq. 2 and 4) represent the independent risks of mortality due to juvenile and senescent factors (respectively). The five parameters (a_1, a_2, a_3, b_1, and b_3) allow considerable flexibility in the shape of this function.

In order to establish a general model which would be appropriate over a wide range of life spans, age is normalized by dividing by longevity. Age was re-expressed as a fraction of longevity, Ω, and hence the use of x/Ω in Equations 2, 3, and 4. No rigorous demographic definition exists for longevity, and it is often taken as the maximum age ever recorded for a species (Altman and Dittmer 1972). We use an alternative definition of longevity as the 99th percentile of the age distribution of a sample. Thus, one percent of a sample would be older than the age we define as longevity. In the Appendix we show that our definition is less dependent on sample size than is a definition based on the maximum age observed. In the Appendix we also show that when senescent mortality factors are strong, this parameter, Ω, can be estimated accurately with relatively small sample sizes.

Discrete-time notation—Considerable notational confusion has arisen in discrete-time parameterizations (Goodman 1982); hence, we will be explicit and use the Leslie matrix notation of Caswell (1989) for a birth-pulse population with postbreeding census. We consider only female life history parameters. No mention will be made of male mortality patterns except to say that they may be quite different from female patterns.

Parenthetical notations denote continuous time and subscripts denote discrete time. The survivorship from birth to age x is $l(x)$. The fecundity rate, F_x, is estimated as the product of the probability that a female of age x survives one time step, P_x, and the number of offspring produced by a surviving female (B_x or the crude birth rate). The asymptotic population growth rate, λ, is calculated by solving the discrete-time equivalent of Lotka's equation (eq. 17 in Goodman 1982; eq. 5.16 in Caswell 1989). The frequency of animals in a sample belonging to age class x is denoted by n_x.

Parameter estimation—Parameters of the mortality model were fit using a maximum likelihood approach. At stable age distribution, the probability density function for observing an individual of age x is given by:

$$\text{p.d.f.}(x) = \frac{l(x)}{\int_0^\infty l(y)\,dy}.$$

Because a closed-form solution to the above integral does not exist for the Siler survivorship function, the following approximation was used:

$$\text{p.d.f.}(x) = \frac{l(x)}{\sum_{i=0}^{\omega} l(i)},$$

where ω was chosen as 1.5 times Ω (a point at which $l(\omega)$ is, for all practical purposes, zero). The likelihood function is given by the joint probability of obtaining the observed age-frequency distribution, $\boldsymbol{n}$. This was estimated as

$$L(\boldsymbol{n}\,|\,a_1, a_2, a_3, b_1, b_3) = \prod_{i=1}^{\omega} [\text{p.d.f.}(x_i)]^{n_i},$$

where x_i represents the true age of individuals in age class i. The values of parameters a_1 to b_3 were chosen to maximize the natural logarithm of L using the Simplex algorithm (Press *et al.* 1988:289).

Fur seal model—We chose the northern fur seal as the species on which to base a general model of marine mammal survivorship. A wealth of life history information exists for this species over a long time period. We use the fur seal data presented by Smith and Polacheck (1981). Population size was relatively constant during the 1950s, and thus population parameters taken from 1958–1961 should be representative of a population with an approximately stationary age distribution (Smith and Polacheck 1981). (Female fur seals may have been harvested in the 1950s (D. Chapman, personal communication), however those harvests are assumed to be negligible.) Pooling age distributions over a 4-yr period should smooth any deviations from stable age distribution owing to observed annual variation in births (Chapman 1964).

The age frequency distribution for age classes 9 to 20 (Table 1) was estimated from female seals taken by U.S. researchers from 1958 to 1961 (table 1 in Smith and Polacheck 1981). Because juveniles were underrepresented in this sample, age classes 1 to 8 were treated as missing. The expected frequencies in age classes 4 to 8 were calculated using an iterative fitting procedure. First, the expected frequencies in age classes 4 to 8 were estimated based on the 478 animals observed in age class 9 and assuming a survival rate of 0.95 for age classes 4 to 8 (this is one of several estimates proposed by Smith and Polacheck for these age classes). Then the expected frequency in age class 1 was estimated based on observed pregnancy rates of females in age classes 4 to 20. The number in age class 1 was thus the product of age frequencies and crude birth rates over

Table 1. Age-frequency distribution, crude birth rates, fecundity rates and survival rates for northern fur seals, 1958–1961. Estimated age frequencies are given in parentheses. Survival rates were calculated by fitting the 5-parameter version of the Siler survivorship model to the age frequency distribution. Fecundity rates were estimated as the product of these survival rates and the crude birth rates.

Age (years)	Age class x	Age frequency n_x	Birth rate B_x	Survival rate P_x	Fecundity rate F_x
0	1	(2,096)	0.000	0.539	0.000
1	2		0.000	0.702	0.000
2	3		0.015	0.814	0.012
3	4	(646)	0.015	0.885	0.013
4	5	(572)	0.220	0.928	0.204
5	6	(530)	0.395	0.951	0.376
6	7	(505)	0.395	0.964	0.381
7	8	(486)	0.425	0.969	0.412
8	9	478	0.460	0.969	0.446
9	10	447	0.445	0.964	0.429
10	11	434	0.450	0.956	0.430
11	12	429	0.440	0.943	0.415
12	13	387	0.430	0.923	0.397
13	14	362	0.420	0.894	0.376
14	15	336	0.410	0.854	0.350
15	16	293	0.390	0.799	0.312
16	17	233	0.330	0.726	0.239
17	18	142	0.355	0.631	0.224
18	19	97	0.265	0.515	0.136
19	20	59	0.255	0.384	0.098
20	21		0.000	0.000	0.000

age classes 4 to 20. The Siler survivorship curve was then fit to the estimated age distribution, and the expected frequencies in age classes 4 to 8 were re-estimated based on the best fit to the model. The expected frequency in age class 1 was re-estimated, and the fitting procedure was repeated until the expected frequencies in age classes 4 to 8 did not change between iterations.

Alternative model life tables—Although the fur seal model may be an adequate model life table for many pinniped species, it may not be for cetaceans. Unfortunately, insufficient information currently exists to develop a model life table based on actual data for any species of cetacean. Two alternative model life tables were used, based on species with life history traits more similar to cetaceans. The first is a published Siler model based on aggregate data from several species of Old World monkey (Gage and Dyke 1988); parameter values given in Table 2 are equal to their published values multiplied by a longevity of 34 yr. The second model life table was based on human females in the United States circa 1900; Siler parameters (Table 2) were estimated by fitting a tabular life table (Fruehling 1982), scaled to a longevity of 81 yr.

Spotted dolphin example—Spotted dolphins commonly occur with yellowfin tuna in the eastern tropical Pacific. Dolphin mortality has resulted from the activities of the tuna purse-seine fishery in this area, and one spotted dolphin population (the "northern offshore stock," Perrin *et al.* 1979) was estimated

Table 2. Estimates of survival rate parameters for northern fur seals, Old World monkeys, and human females based on the Siler model (Eq. 1). In deriving these estimates, ages were scaled by an estimate of longevity, Ω (18 yr for fur seals, 34 yr for monkeys, and 81 yr for humans).

Species	a_1	a_2	a_3	b_1	b_3
Northern fur seal female	14.343	0.1710	0.0121	10.259	6.6878
Old World monkeys	30.430	0.0000	0.7276	206.720	2.3188
Human female	40.409	0.4772	0.0047	310.360	8.0290

to have decreased to between 29% and 47% of their historical abundance by 1979 (Smith 1983). Based on the ecological concept of density compensation, such populations would be expected to respond to such harvests with increased per-capita growth rates. Here we use measured reproductive parameters and our mortality estimation procedure to estimate possible ranges in the current growth rate of this spotted dolphin population.

Reproductive rates were measured from specimens collected by technicians aboard tuna vessels. The mean age of sexual maturity for females is approximately 12 yr (Myrick *et al.* 1986). Given an 11.5-mo gestation time (Perrin *et al.* 1976), the mean age at first birth is approximately 13 yr if females become pregnant soon after their first ovulation. The fraction of mature females that were pregnant in 1974–1983 samples is estimated as 0.290 (Barlow 1985). Dividing by gestation time (0.958 yr) and assuming a sex ratio of 50% females and a litter size of one (Perrin *et al.* 1976), the crude female birth rate, B_x, is estimated as 0.152 for all mature age classes.

Survival rates could not be calculated directly from age distributions due to apparent biases in sampling (Hohn and Scott 1983). Instead, survival rates were calculated from estimates of longevity and using several possible models for the shape of the survivorship function. Estimates of longevity (the age of the 99th percentile of an aged sample) for spotted dolphins range from approximately 33 yr in the eastern Pacific (n = 806, from fig. 2 in Myrick *et al.* 1986) to 45 yr in the western Pacific (n = 200, from fig. 16 in Kasuya 1976). To allow for uncertainty in age estimation procedures, both values are considered as estimates of Ω. A range is used for the parameters of the mortality model, including survivorship curves (Fig. 1) based on: (1) the fur seal model, (2) the Old World monkey model, and (3) the human female model.

Harbor porpoise example—Harbor porpoise are often caught and die in coastal gill-nets which are set for halibut in central California (Barlow 1987). For management of this species, it would be useful to know the upper limits on the rate of population growth. No data exist on the age distribution of harbor porpoise in central California, and very few data exist on reproductive rates. We therefore use data collected from other harbor porpoise populations to estimate maximum feasible rates of population growth.

Most of what is known about harbor porpoise life history is based on studies in eastern Canada. Based on tooth layer counts from a sample of 120 males and females from that area, the maximum observed age was 13 yr and the 99th percentile of the age distribution was 10 yr (derived from fig. 3, 4 in Gaskin

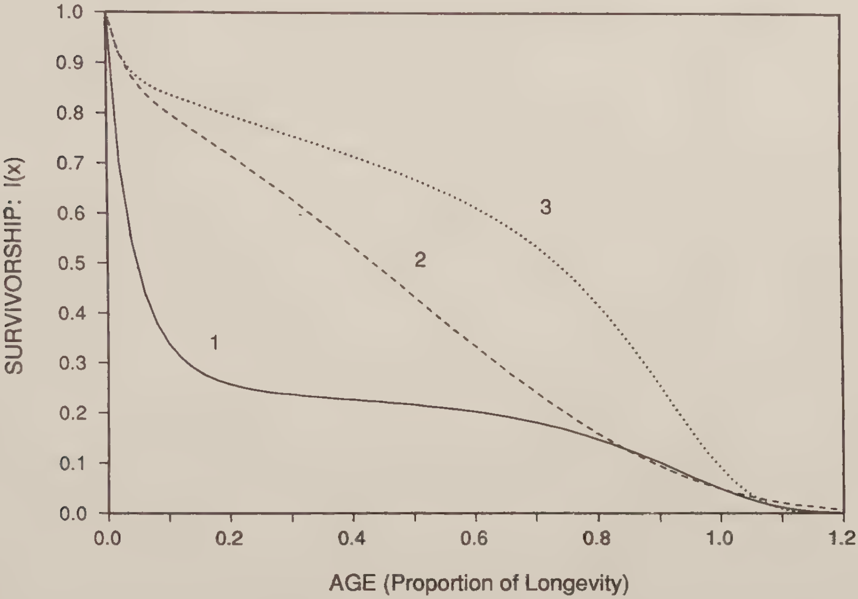

Figure 1. Survivorship curves based on three models: (1) female northern fur seals, (2) larger Old World monkeys, and (3) human females circa 1900. Parameter values for the Siler model (Eq. 1) are given in Table 2. Age is expressed as proportion of longevity, Ω.

and Blair 1977). Harbor porpoise mature at approximately 3 to 5 yr (Gaskin *et al.* 1984, Read 1989). Most estimates of gestation time rage from 10 to 11 mo for all porpoise species (Gaskin *et al.* 1984). Therefore, a female maturing at age 3 could first give birth at age 4. Simultaneously pregnant and lactating females have been found in samples from several populations (Gaskin *et al.* 1984), indicating that mature females may give birth every year. This is verified by cases where individually recognized females were accompanied by different calves in consecutive years (Watson 1976, B. Taylor, personal communication). In most studies, however, the percentage of mature females that was simultaneously pregnant and lactating is less than 100% (Gaskin *et al.* 1984, Read 1989), indicating an average calving interval of greater than 1 yr.

Upper bounds on the maximum rates of population growth were estimated using the ranges in the above parameters that would yield the largest growth rate. Longevity, Ω, was taken as 10 yr. The age at first birth was taken as 4 yr. The calving interval was taken as 1 yr. Again, a range was used for the parameters of the mortality model; survival rates were estimated based on the same three models used above for spotted dolphins (Fig. 1).

RESULTS

Fur seal—The maximum likelihood fit of the 5-parameter Siler model to the age-frequency distribution for fur seals is shown in Figure 2. The model

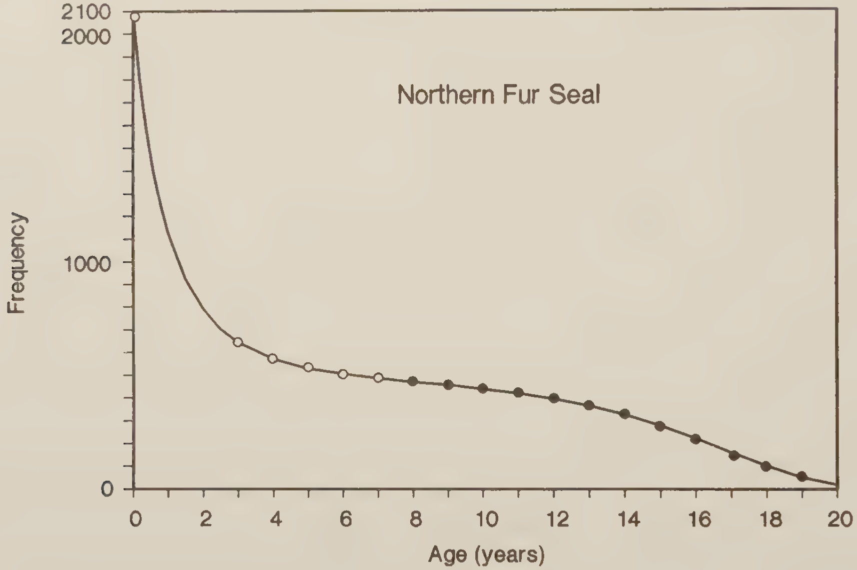

Figure 2. Survivorship curve for female northern fur seals, 1958–1961, based on maximum likelihood fit of the Siler model to an estimated age-frequency distribution. Solid circles represent observed frequencies at age and open circles represent estimated frequencies based on reproductive rates and iterative fitting algorithm (see text).

gave a very good fit to the data ($\chi^2 = 5.65$, df = 12, $P = 0.933$; Kolmogorov/Smirnov (K/S) test, $P = 0.920$). The parameter values which resulted in the best fit are given in Table 2, and the resulting estimates of survival rates are given in Table 1. Leslie-matrix fecundity rates were calculated as the adult survival rates times the raw pregnancy rates (Table 1). As a check on internal consistency, population growth rates were calculated using these survival and fecundity rates. As expected, the resulting finite rate of population growth ($\lambda = 1.0002$) indicates that net growth is effectively zero.

Spotted dolphin—Estimates of current population growth rate for spotted dolphins are given in Table 3 based on three different models of survivorship and based on longevity estimates of 33 and 45 yr. Population growth rates are less than 1.0 for the fur seal model with longevities of 33 or 45 yr and for the monkey model with longevity of 33 yr. Because the offshore spotted dolphin population has been reduced by tuna fishing operations, one might expect that (in the absence of continued fishing mortality) density dependent responses would result in values for life history parameters that yield a growth rate greater than 1.0. The other three combinations of survivorship and longevity result in growth rates greater than 1.0. The maximum growth rate expected given the most optimistic survivorship schedule (that patterned after a human population) and the higher estimate of longevity is 4.2% per year. This approximately equals the maximum rate of increase estimated by Reilly and Barlow (1986) for a

Table 3. Estimates of population growth rate, λ, for spotted dolphins based on current estimates of reproductive rates, three models of survivorship, and two estimates of longevity. Parameters of survivorship models are given in Table 2.

Survivorship model	Longevity	
	$\Omega = 33$ yr	$\Omega = 45$ yr
Northern fur seal	0.972	0.996
Old World monkeys	0.992	1.020
Human	1.024	1.042

dolphin which first gives birth at 13 yr and which has a calving interval of 3 yr (their fig. 4*b*).

Harbor porpoise—Maximum rates of population growth for harbor porpoise were estimated as 0.917, 0.989, and 1.094 (respectively for the fur seal, Old World monkey, and human survivorship models). If assumptions are met (*i.e.,* longevity is 10 yr and females produce one calf per year starting at 4 yr of age), scaled survival rates must be higher than those of fur seals or Old World monkeys in order for porpoise populations to grow. In the most optimistic case, a population growth rate of 9.4% is possible if survivorship is patterned after a human population.

Discussion

The method of estimating mortality rates for populations based on scaling the survivorship curves of other populations is not meant as a substitute for directly measuring mortality. Rather, it is an attempt to improve the method by which mortality is modeled when such direct measures are not available. We envision the primary use of our approach will be in exploratory modeling such as in our examples of spotted dolphins and harbor porpoise. We do not recommend this approach for estimating the actual population growth rate for any population.

Advantages of age-specific rates—In most previous formulations, demographic models of marine mammals have used survival rates which are constant over all adult age classes (Allen 1981, Breiwick *et al.* 1984, Reilly and Barlow 1986). Although it is usually acknowledged that senescent mortality is expected in mammals, mathematical simplicity has taken precedence over biological reality. This is not a fatal flaw in such studies. As shown by Goodman (1984), population growth rates can be accurately estimated from a model which assumes constant adult survival and fecundity, regardless of the fact that both may show age-specific patterns. Furthermore, Goodman (1984) showed how to estimate one survival parameter that results in essentially the same first-order (*i.e.,* static) behavior as would the full age-specific model. The problem with this approach is that the resulting survival parameter is a theoretical construct which has lost intuitive biological meaning.

The difficulty in dealing with an adult survival parameter which has lost biological meaning is illustrated in the paper by Reilly and Barlow (1986). They estimate maximum population growth rates for dolphins based on a range of estimates of reproductive rates and calf and non-calf survival rates. The major problem they confronted was in determining a realistic upper range for non-calf survival rate. They assumed a maximum age of 50 yr. They showed that survival rates greater than 0.97 resulted in greater than 22% of their populations reaching this maximum age. Although, as they noted, this seems unreasonable, the survival parameter they used is a mathematical abstraction and is not necessarily subject to what seems to be biologically reasonable constraints. Their arguments are, therefore, weak and are based too strongly on their somewhat loosely defined concept of maximum life span.

Biological limits to survival rates are much more apparent using the approach outlined above for spotted dolphins. Senescence appears to be genetically programmed, and thus longevity is largely predetermined. Longevity thus acts as one very obvious biological limit to survival rates. Survivorship curves of mammals all have a similar shape (juvenile risks are high but decrease rapidly; senescent risks increase rapidly). This shape also imposes limits to survival rates. Finally, within the family of shapes which are possible, one can pick a survivorship curve which represents the maximum survival in a protected environment. For the latter we chose the survivorship curve for human females circa 1900 (*i.e.,* during the period of good data collection methods and before the advent of most modern medicines). We believe that this shape reflects an absolute limit to the likely survivorship of any wild population.

Given available information, we cannot evaluate whether the shape of the survivorship curve for the northern fur seal population is truly representative of marine mammals. It was chosen as the only marine mammal species for which data were of the quality and quantity necessary to establish a model. A better approach would be to base a model on a mean survivorship curve from a variety of marine mammals or possibly from a variety of other large mammals with similar life history traits to the species being studied. The life history of dolphins appears more similar to that of humans or elephants (long life span and long interval between offspring) than that of fur seals. We hope that as additional information becomes available for other species, we will be able to specify better a general model of survivorship for marine mammals or, possibly, separate models for pinnipeds and cetaceans. We believe, however, that use of model life tables for marine mammals is a significant improvement over the usual assumption of constant mortality for all age classes.

Scaling by longevity—The idea of scaling survivorship curves to compare species is an old one, dating back at least to the work of Pearl and Parker (1921). In a later paper, Pearl (1922) used a method similar to ours and scaled by the age at which survivorship falls to some small fraction of the first age class. That method was criticized on the basis of high sampling variability (Greenwood 1928). Another method was introduced by Pearl and Miner (1935) based on scaling by the mean duration of life. In the latter paper, the authors were able to note the similarities of life tables for roaches, fruit flies, mice, and automobiles by plotting all on the same graph. More recently, Eberhardt (1985) suggested the possibility of scaling by the modal age of senescence, as defined by Siler (1979).

None of the previous approaches used to scale survivorship curves were appropriate for our study. Rescaling based on the modal age of senescence was not chosen because it requires prior fitting of a Gompertz model to the senescent phase of a survivorship curve (Siler 1979). We desired a method that would allow us to rescale age prior to fitting a survivorship curve. Rescaling based on the mean duration of life was not chosen because this can be greatly affected by the juvenile mortality phase. We wanted a method that would be anchored more strongly at the other end of the age scale and which would thus retain the expected relationships between juvenile, adult, and senescent phases of life. The method used by Pearl (1922) was not quite appropriate either, because it assumed that samples were taken from a cohort study. Given a sample from an age frequency distribution it is not possible to estimate the age at, say, 1% survivorship unless the survivorship curve is first estimated.

Instead of the age at 1% survivorship, we chose a scaling factor based on the 99th percentile of an aged sample. This statistic is likely to have similar properties to the former (proposed by Pearl 1922). Contrary to arguments made by Greenwood (1928), our simulation studies (Appendix) show that this statistic can be accurately estimated with small sample sizes. Because senescent mortality is a dominant force in mammalian life tables and because it increases so rapidly, we expect this result to hold for any mammal population in which some of its members live long enough to experience senescence. Our approach may fail for some populations in which harvesting truncates the age distribution before senescence, as may be the case for harvested deer populations (Barlow and McCulloch 1984, Eberhardt 1985). We have not investigated the problem of estimating longevity from non-stable age distributions; however, if senescence is strong, we do not believe that this is a significant problem.

Using prior expectations in estimating mortality rates—We have concentrated our attention on situations (1) where large quantities of data exist and a full Siler model can be fit (*e.g.*, the fur seal) or (2) where very little data exist and a model life table is substituted (*e.g.*, the spotted dolphin and harbor porpoise). A third situation arises when some data exist, but not enough to reliably fit a 5-parameter model. In such situations one would like to combine the information in the available data with the information contained in the model life table to obtain a realistic survivorship curve. We propose three possible methods for estimating mortality rates in such situations.

The simplest method would give equal weight to both the actual data and the model life table. Assume that the actual data is the age distribution of *n* individuals taken randomly from a stable population. The expected stable age distribution for *n* individuals is calculated from the appropriate model life table and is combined with the observed age distribution. The Siler model is then fit to the combined age distribution.

A second alternative would be to fit only a portion of the Siler parameters based on the actual data. The remaining parameters could be held constant at whatever values are specified in the model life table. The most variable parameter could be fit first (*e.g.*, the juvenile mortality parameter a_1), and the goodness of fit could be evaluated. Additional parameters could be added in a stepwise fashion until the improvement in the goodness of fit is no longer significant.

A final alternative would be to use an empirical Bayesian approach (Iversen 1984) with the Bayesian prior distribution defined by the model life tables. Rather than use a single model life table, the prior expectations of mammalian survivorship could be represented as a probability distribution for each of the 5 parameters in the Siler model. Because this model is rather over specified (Siler 1983), covariances between the parameters would also have to be considered. The result of this approach would be a probability distribution of survival rates which is a function of both the data and the prior distributions. As more data are included, the importance of the prior distributions will diminish.

Future research is planned to investigate each of the above approaches for estimating survival rates.

Literature Cited

Allen, K. R. 1981. Application of population models to large whales. Pages 263–276 *in* C. W. Fowler and T. D. Smith, eds. Dynamics of large mammal populations. John Wiley and Sons, New York, NY.

Altman, P. L., and D. S. Dittmer, eds. 1972. Biology data book, Second edition, Vol. I. Federation of American Societies for Experimental Biology, Bethesda, MD.

Barlow, J. 1985. Variability, trends, and biases in reproductive rates of spotted dolphins, *Stenella attenuata*. Fishery Bulletin 83:657–669.

Barlow, J. 1987. An assessment of the status of harbor porpoise populations in central California. Administrative Report LJ-87-06, available from Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038, USA. 35 pp.

Barlow, J., and C. Y. McCulloch. 1984. Recent dynamics and mortality rates of the Kaibab deer herd. Canadian Journal of Zoology 62:1805–1812.

Breiwick, J. M., L. L. Eberhardt and H. W. Braham. 1984. Population dynamics of western Arctic bowhead whales (*Balaena mysticetus*). Canadian Journal of Fisheries and Aquatic Sciences 41:484–496.

Caswell, H. 1989. Matrix population models: construction, analysis, and interpretation. Sinauer Associates, Sunderland, MA.

Caughley, G. 1966. Mortality patterns in mammals. Ecology 47:906–918.

Caughley, G. 1977. Analysis of vertebrate populations. John Wiley & Sons, Chichester, U.K.

Chapman, D. G. 1964. A critical study of Pribilof fur seal population estimates. Fishery Bulletin 63:657–669.

de la Mare, W. K. 1986. On the estimation of mortality rates from whale age data, with particular reference to minke whales (*Balaenoptera acutorostrata*) in the Southern Hemisphere. Report of the International Whaling Commission 36:239–250.

Eberhardt, L. L. 1985. Assessing the dynamics of wild populations. Journal of Wildlife Management 49:997–1012.

Fruehling, J. A., ed. 1982. Sourcebook on death and dying. Marquis Professional Publications, Chicago.

Gage, T. B. 1988. Mathematical hazard models of mortality: an alternative to model life tables. Americal Journal of Physical Anthropology 76:429–441.

Gage, T. B., and B. Dyke. 1986. Parameterizing abridged mortality tables: the Siler three-component hazard model. Human Biology 58:275–291.

Gage, T. B., and B. Dyke. 1988. Model life tables for the larger Old World monkeys. American Journal of Primatology 16:305–320.

Gaskin, D. E., and B. A. Blair. 1977. Age determination of harbour porpoise, *Phocoena phocoena* (L.), in the western North Atlantic. Canadian Journal of Zoology 55: 18–30.

Gaskin, D. E., G. J. D. Smith, A. P. Watson, W. Y. Yasui and D. B. Yurick. 1984. Reproduction in the porpoises (Phocoenidae): implications for management. Reports of International Whaling Commission (Special Issue 6):135–148.

Goodman, D. 1978. Management implications of the mathematical demography of long lived animals. Contract report prepared for the Marine Mammal Commission. NTIS PB-289678. 80 pp.

Goodman, D. 1980. Demographic intervention for closely managed populations. Pages 171–195 *in* M. E. Soulé and B. A. Wilcox, eds. Conservation biology: an evolutionary-ecological perspective. Sinauer Associates, Sunderland, MA.

Goodman, D. 1982. Optimal life histories, optimal notation, and the value of reproductive value. American Naturalist 119:803–823.

Goodman, D. 1984. Statistics of reproductive rate estimates, and their implications for population projection. Reports of the International Whaling Commission (Special Issue 6):161–173.

Greenwood, M. 1928. "Laws" of mortality from the biological point of view. Journal of Hygiene 28:267–294.

Hohn, A. A., and M. D. Scott. 1983. Segregation by age in schools of spotted dolphin in the eastern tropical Pacific. Abstract, Fifth Biennial Conference on the Biology of Marine Mammals, Boston, MA. November 27–December 1, 1983.

Iversen, G. R. 1984. Bayesian statistical inference. Sage Publications, Inc., Beverly Hills, CA.

Kasuya, T. 1976. Reconsideration of life history parameters of the spotted and striped dolphins based on cemental layers. Scientific Report of the Whales Research Institute 23:73–106.

Myrick, A. C., Jr., A. A. Hohn, J. Barlow and P. A. Sloan. 1986. Reproductive biology of female spotted dolphins, *Stenella attenuata,* from the eastern tropical Pacific. Fishery Bulletin 84:247–259.

Paranjpe, S., and M. B. Rajarshi. 1986. Modelling non-monotonic survivorship data with bathtub distributions. Ecology 67:1693–1695.

Pearl, R. 1922. Experimental studies on the duration of life. VI. A comparison of the laws of mortality in *Drosophila* and in man. American Naturalist 56:398–405.

Pearl, R., and J. R. Miner. 1935. Experimental studies on the duration of life. XIV. The comparative mortality of certain lower organisms. Quarterly Review of Biology 10:60–79.

Pearl, R., and S. L. Parker. 1921. Experimental studies on the duration of life. I. Introductory discussion of the duration of life in *Drosophila.* American Naturalist 55:481–509.

Perrin, W. F., J. M. Coe and J. R. Zweifel. 1976. Growth and reproduction of the spotted porpoise, *Stenella attenuata,* in the offshore eastern tropical Pacific. Fishery Bulletin 74:229–269.

Perrin, W. F., P. A. Sloan and J. R. Henderson. 1979. Taxonomic status of the "southwestern stocks" of the spinner dolphin, *Stenella longirostris,* and the spotted dolphin, *S. attenuata.* Report of the International Whaling Commission 29:175–184.

Press, W. H., B. P. Flannery, S. A. Teukolsky and W. T. Vetterling. 1988. Numerical recipes: the art of scientific computing. Cambridge University Press, Cambridge, U.K.

Read, A. J. 1989. Incidental catches and life history of harbour porpoises *Phocoena phocoena* from the Bay of Fundy. Ph.D. dissertation, University of Guelph, Canada. 121 pp.

REILLY, S. B., AND J. BARLOW. 1986. Rates of increase in dolphin population size. Fishery Bulletin 84:527–533.

SILER, W. 1979. A competing-risk model for animal mortality. Ecology 60:750–757.

SILER, W. 1983. Parameters of mortality in human populations with widely varying life spans. Statistics in Medicine 2:373–380.

SMITH, T. D. 1983. Changes in size of three dolphin (*Stenella* spp.) populations in the eastern tropical Pacific. Fishery Bulletin 81:1–13.

SMITH, T., AND T. POLACHECK. 1981. Reexamination of the life table for northern fur seals with implications about population regulatory mechanisms. Pages 99–120 *in* C. W. Fowler and T. D. Smith, eds. Dynamics of large mammal populations. John Wiley and Sons, New York, NY.

SPINAGE, C. A. 1972. African ungulate life tables. Ecology 53:645–652.

WATSON, A. P. 1976. The diurnal behavior of the harbour porpoise (*Phocoena phocoena* L.) in the coastal waters of the western Bay of Fundy. M.Sc. thesis, University of Guelph, Canada. 93 pp.

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APPENDIX

Sensitivity of Ω *to sample size*—A sample of n ages (X_i: $i = 1, 2, 3, \ldots, n$), drawn at random from a population with a particular age distribution and ordered such that $X_{i-1} < X_i < X_{i+1}$, is set of "order statistics" for age. In a sample of 100 ages, the 99th order statistic could be called the "99th percentile" because 99 percent of the sample values are smaller than or equal to the value of the 99th order statistic. The maximum order statistic of a sample (of any size) could be called the "100th percentile" because 100 percent of the sample ages are less than or equal to the maximum age.

For a sufficiently simple age distribution, such as one resulting from an age-constant mortality rate, the sampling properties of the order statistics and percentiles could be determined analytically. However, for more complex survivorship functions like those represented by the Siler model, computer simulation is a more tractable technique to investigate sampling behavior.

Figure 3 shows the results of simulated sampling from the age distribution of a hypothetical population which is stable and stationary and subject to the fur seal model survivorship schedule. For a particular sample size, represented on the X-axis, 250 random samples were drawn from the hypothetical age distribution. The mean of the largest ages is represented in Figure 3 as the "100th percentile" with error bars to indicate ±1 standard deviation of the observed largest values. The curve labelled "99th percentile" represents the expected values for our parameter Ω, again with ±1 standard deviation (based on 250 samples independent of those used to estimate other percentiles). The analogous curve for the 95th percentile is also shown.

As seen in Figure 3, the 99th percentile of a random sample from the fur seal model is less sensitive to sample size and less variable than the maximum age (100th percentile). Further decreasing the percentile rank to 95 results in even less sensitivity to sample size. However, we chose the 99th percentile as a scaling value because percentile ages of lower rank will be more heavily influenced

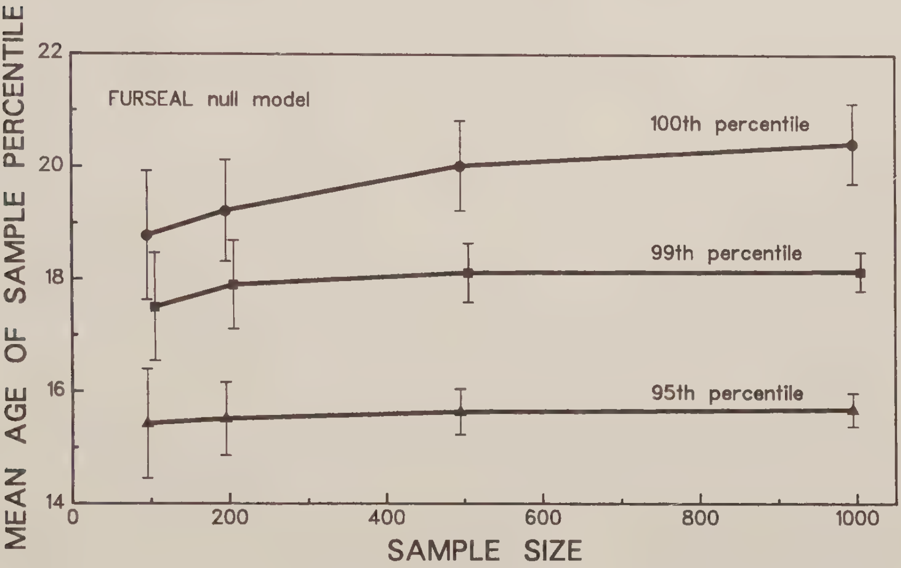

Figure 3. Mean values for selected percentile ranks in samples of various sizes from the "fur seal model" age distribution. Means and error bars (±1 standard deviation) were computed from 250 samples at each sample size.

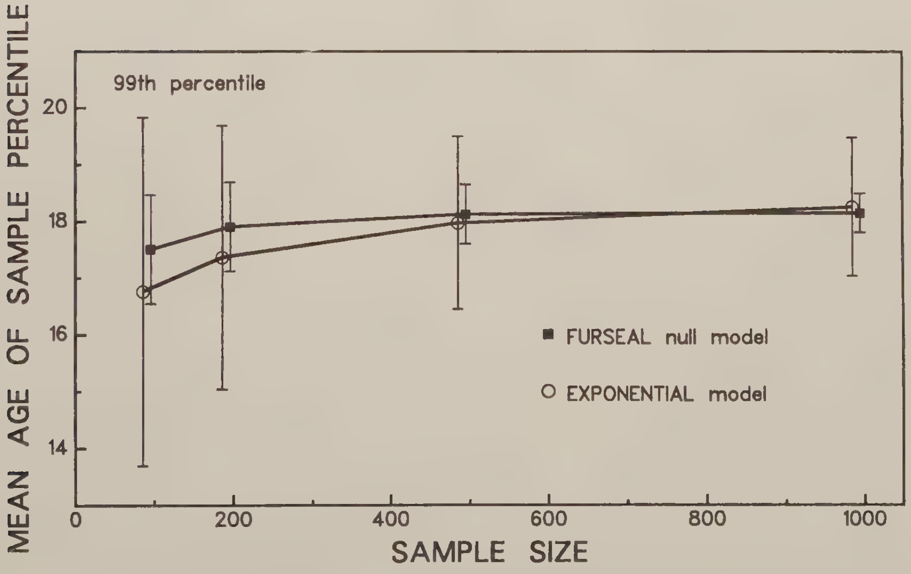

Figure 4. Mean values of the 99th percentile ages versus sample size for a survivorship schedule with increased senescent mortality (fur seal model) and a schedule with constant mortality (exponential model). Means and error bars (±1 standard deviation) were computed from 250 samples of each sample size.

by mortality patterns early in life. We also believe that the 99th percentile will be less sensitive to deviations from stable age distribution than would be a lower percentile. Thus, it is desirable to base the scaling on as large a fraction of the life span as possible.

Effect of senescent mortality—To illustrate the effect that senescent mortality factors have on the age distribution (and consequently on the sampling properties of Ω), we compared a constant mortality model with the fur seal model (Fig. 4). Both models had age distributions with the 99th percentile equal to 18 yr. The fur seal model, which exhibits senescent mortality, results in estimates of Ω which are less sensitive to sample size and much less variable than those obtained by sampling the exponential age distribution (which is not subject to increasing mortality due to senescence).

Conclusion—Although these examples do not constitute general proofs, we believe that the results will hold for most survivorship schedules characteristic of marine mammal species. The 99th percentile of a sample will be less sensitive to sample size (for samples of 100 or more) than the maximum age and will have lower variance. Senescent increase in the mortality rate will serve to stabilize the sampling properties of any of the higher order statistics (or percentile ranks) for age.

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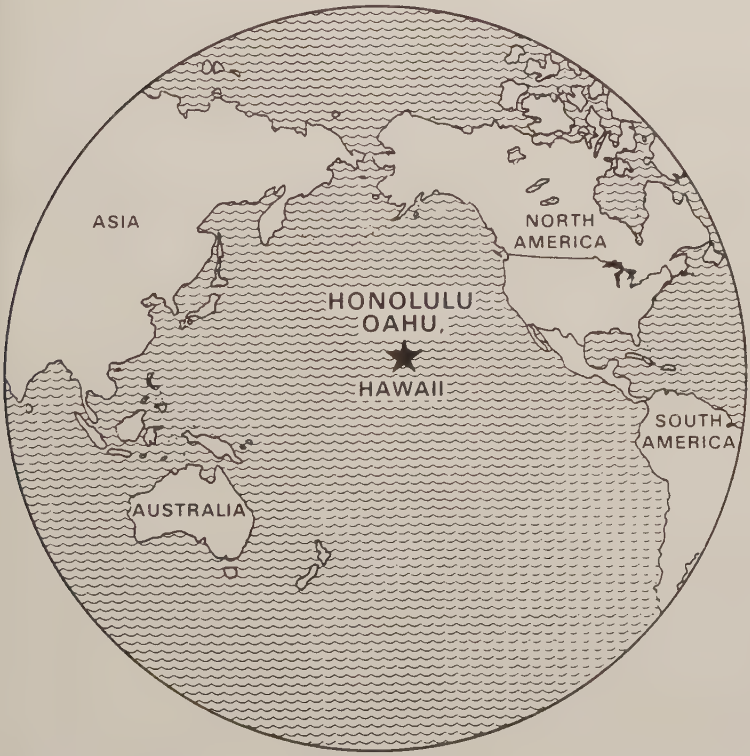
Laboratory Objectives

The Honolulu Laboratory (1) provides needed scientific information and expertise to the Western Pacific Regional Fishery Management Council in the preparation of Fishery Management Plans for resources in the U.S. Fishery Conservation Zone around Hawaii, American Samoa, and Guam in the central and western Pacific; (2) conducts studies to delineate and assess the nearshore marine resources of the Northwestern Hawaiian Islands and other island areas of direct interest to the United States; and (3) investigates the population dynamics and status of stocks, behavior and physiology, and the environmental influence on the ecology of the offshore pelagic species of commercial importance such as the tunas and billfishes.

Personnel

George W. Boehlert, Laboratory Director
Jerry A. Wetherall, Chief, Pelagic Resources Investigation
Jeffrey J. Polovina, Chief, Insular Resources Investigation
William G. Gilmartin, Chief, Marine Mammals and Endangered Species Program
Samuel G. Pooley, Chief, Fishery Management Research Program



Areas of Expertise

Physiology, behavior, bioenergetics, and ecology of pelagic fishes, particularly tunas; population dynamics and stock assessment of pelagic species, marine mammals, and endangered species; population dynamics and trophic interactions of nearshore marine fish and invertebrate complexes; biology, ecology, and life history of offshore pelagic fishes; and fishery economics.

Laboratory Features

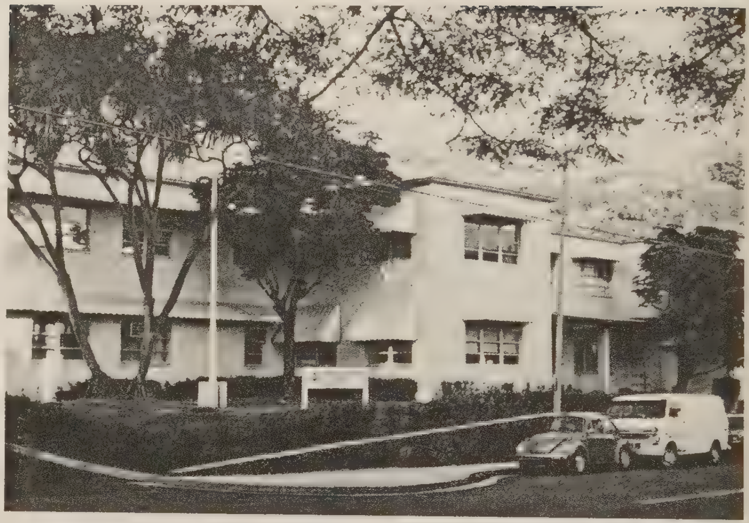
The Honolulu Laboratory was built in 1950 on a site adjacent to the University of Hawaii on land deeded to the U.S. Government by the state of Hawaii. The Laboratory is located in the capitol of the state of Hawaii, on the island of Oahu, which is the hub of all activity in the state. Hawaii's mid-Pacific location makes the Honolulu Laboratory ideally situated to study the widely distributed, economically important species of large fishes such as the tunas and billfishes.

The Laboratory's Kewalo Research Facility includes a building of 10,800 square feet, which houses offices and laboratories tailored for various research activities, a machine shop, and storage areas. On the adjoining grounds is a saltwater well and aerating system that has the capacity to produce over 1,000 gallons per minute of high-quality coral-filtered seawater. This seawater supplies various tanks, including a series of five 20,000-gallon circular pools that can be observed from a tower, a 200,000-gallon oceanarium, and specially designed experimental tanks of various sizes. These facilities are on a 0.98 acre area at the southeast entrance of Kewalo Basin, the base for the Hawaiian skipjack tuna fleet. The Kewalo Research Facility is the only research center in the world that is able to collect and maintain live tunas throughout the year for use in behavioral and physiological research. To investigate the nearshore and offshore pelagic fish resources, the NOAA ship *Townsend Cromwell* is presently assigned to the Honolulu Laboratory.

Laboratory History

The inception of the Honolulu Laboratory, first known as the Pacific Oceanic Fishery Investigations (POFI), can be traced to Public Law 329 (1947), which authorized the exploration, investigation, and development of high-seas fisheries of the territories and island possessions of the United States in the tropical and subtropical Pacific Ocean and intervening seas. Funds for the Laboratory became available in July 1948 and, in August 1948, POFI was organized and a temporary headquarters office was established in San Francisco. In 1950 POFI moved into its nearly completed laboratory building, adjacent to the University of Hawaii in Honolulu's historic Manoa Valley.

The Laboratory was under the Fish and Wildlife Service in the Department of the Interior from 1948 to 1970. In 1970 the Laboratory came under the newly organized National Marine Fisheries Service, NOAA, in the Department of Commerce and, in 1971 it became a part of the Southwest Fisheries Science Center under the same organizational structure. During the course of its existence, the Honolulu Laboratory has operated the following research vessels: *Henry O'Malley*, *John R. Manning*, *Hugh M. Smith*, *Charles H. Gilbert*, and *Townsend Cromwell*.



Honolulu Laboratory.

Cooperating Agencies

Hawaii's Division of Aquatic Resources, American Samoa's Office of Marine Resources, Guam's Division of Aquatic and Wildlife Resources, Fish and Wildlife Service, Western Pacific Regional Fishery Management Council, University of Hawaii, University of Guam, Bernice P. Bishop Museum, Oceanic Institute, Pacific Tuna Development Foundation, Indian Ocean Fisheries Commission, Indo-Pacific Fisheries Commission, South Pacific Commission, Far Seas Fisheries Research Laboratory (Japan), Commonwealth Scientific and Industrial Research Organization (Australia), Fisheries Research and Development Agency (Republic of Korea), and New Zealand Ministry of Agriculture and Fisheries.

George W. Boehlert

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Oxygen consumption of gestating female *Sebastes schlegeli*: estimating the reproductive costs of livebearing

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Synopsis

During gestation, live-bearing fishes incur physiological energy costs, including provision of energy and respiratory gases to the developing embryos and removal of waste products. Fecundity in the genus *Sebastes* is high, and the ovaries represent a significant portion of the weight of gestating females. In this study, we compare oxygen consumption of gestating females with non-gestating females and males of kurosoi, *Sebastes schlegeli*, to estimate these costs. Oxygen consumption by pregnant females is significantly higher than that of males and immature females at similar sizes and weights. We estimate that a 1.5 kg gestating female consumes 68% more oxygen than a non-gestating fish during the 51.5-day period of gestation. Such an increase in oxygen consumption rates may have important implications to the metabolic scope of gestating females. The additional oxygen consumed by gestating females is greater than that predicted for the embryos alone, suggesting that costs of increased gill ventilation, ionic and osmotic regulation and cardiac output are relatively high. Such energetic costs represent a quantifiable expense of the viviparous mode of reproduction in *Sebastes* as compared with oviparous species.

Introduction

The costs of reproduction in fishes typically involve more than just production of gametes (Wootton 1985). While a variety of adaptations for parental care exist (Balon 1975), live-bearing fishes are faced with the problems of supply of oxygen and nutrients to developing embryos. Hypertrophy of the gas exchange systems of maternal ovaries (Amoroso 1960) and embryos (Webb & Brett 1972, Dobbs 1975) is an example of morphological adaptation, but energetic costs are incurred as well. Several studies have estimated oxygen consumption by embryos in vitro (Moser 1967a, Webb & Brett 1972, Boehlert & Yoklavich 1984, Berglund et al. 1986), but few have considered actual oxygen consumption rates in vivo. These rates may be estimated by considering the relative increase in oxygen consumption by gestating females as compared with spent or immature females or males (Webb & Brett 1972) and may provide insights into the additional costs of reproduction in livebearers.

In the viviparous genus *Sebastes*, oxygen consumption of embryos in vitro increases with developmental stage either linearly (*S. melanops,* Boehlert & Yoklavich 1984) or exponentially (*S. schlegeli*, Boehlert et al. 1986; *S. caurinus*, Dygert & Gunderson 1991). Catabolism during development consumed from 39% (*S. caurinus*) to 88% (*S. schlegeli*) of the initial yolk energy. Gestation times are quite long given the egg size in *Sebastes*; at 10° C, the 0.8 mm egg and embryo of *S. melanops* takes 37 days from fertilization to parturition, whereas the 1.2 mm egg and embryo of *S. schlegeli* takes 51.5 days. The latter is up to 8 times the incubation time of equivalent-sized pelagic eggs (Ware 1975) and 5–8 times longer than for the related lecithotrophic live-bearing scorpaenid *Sebastiscus marmoratus* (Nakanishi 1991). Boehlert et al. (1986) raised the question as to whether oxygen tension inside the ovarian fluid may be considerably lower than ambient values and that estimates of in vitro oxygen consumption may therefore be higher than in vivo rates. A similar problem exists in the oxygen consumption of embryos in gelatinous masses of frog eggs (Burggren 1985). Although *Sebastes* have a very well-developed arterial blood supply system to each ovary (Moser 1967b), the fecundity in this genus is high (Gunderson et al. 1980, Boehlert et al. 1982), and the oxygen demands of the embryos also must be high. In the present study, we estimate the oxygen consumption of embryos in vivo by measuring oxygen consumption of female *S. schlegeli* with gestating embryos as compared with males and non-gestating females, and estimate the relative costs of livebearing in this species.

Materials and methods

Experiments were conducted at the Hokkaido Institute of Mariculture at Shikabe, 4–12 June 1985. Two sources of fish were used. The first was captive stock reared from embryos for periods up to 8 years (Kusakari 1978); the second was fish collected at Otobe in the Sea of Japan on 22 May and 1 June 1985. During the experiments, fish were held in tanks (1.8 × 1.8 × 1.1 m) in running ambient seawater (temperature, 10.6–14.4° C) and starved at least 2 days before use.

Two days prior to the beginning of experiments, fish were weighed and measured, and sex was determined after fish were anesthetized in tricaine methanesulfonate (MS–222, $60\,\mathrm{mg} \cdot \mathrm{l}^{-1}$). (Reference to trade names does not imply endorsement by the National Marine Fisheries Service). Females were catheterized, and developing embryos removed following techniques of Boehlert & Yoklavich (1984). Embryos were staged using scheme described by Yamada & Kusakari (1991). Estimates of time since fertilization (as a function of development stage) were calculated from the equation in Boehlert et al. (1986).

The respirometer consisted of a cylindrical fish chamber constructed of acrylic tubing (20 cm in diameter). One end was sealed with 1.3 cm thick acrylic sheet, except for a small water intake hole. The opposite end had a similar acrylic sheet with a 0.95 cm thick circular piece cut to fit the inner diameter of the cylindrical fish chamber. Silicone sealer and Teflon tape made an effective seal when the chamber was closed and held in place with an elastic band. The respirometer volume was 13.2 l. Incoming water was saturated with air and entered the chamber at one end. At the opposite end, water was collected through tubing and connected to a housing for the oxygen electrode (Takara Thermistor Instrument Co. recording dissolved oxygen meter, Model No. R-F), which was immersed in the water bath. The oxygen electrode was calibrated each morning in air-saturated seawater at the experimental temperature and zeroed in seawater containing potassium metabisulfite.

Prior to an experiment, fish were anesthetized in MS-222 to minimize handling stress and transferred to the respiration chambers, which were then sealed. Fish in the respirometers typically recovered from the anesthesia within 3–5 min and assumed normal orientation; experiments were started at this point. The respirometers were held in a tank (1.8 × 1.1 × 0.65 m), which was filled to maintain a constant flow of air-saturated seawater. The tank was partially covered with black plastic during experiments. Fish activity was visually monitored, and oxygen content of the outflowing water was recorded at 5–10 min intervals. Flow rates (33.84–$92.64\,\mathrm{l} \cdot \mathrm{h}^{-1}$) were adjusted to fish size so that oxygen content in the respirometer typically decreased to equilibrium values after 10–20 min. The experiment was terminated after the oxygen level had not changed over a 10-min period, then ambient oxygen content was determined. Oxygen consumption rates (ml $0_2 \cdot h^{-1}$) were determined by multiplying the change in oxygen concentration of inflowing and outflowing water by the flow rate. For each animal, a mean value of oxygen consumption was computed from two replicates. Experimental periods for each replicate averaged 43 min. Our estimates may be considered routine metabolic rates (Fry 1971). Control experiments were run with empty respirometers, and the drop in oxygen content was negligible.

Although ambient temperatures varied (10.6–14.4° C) during experiments because no temperature control was available, the temperature change during each experiment did not exceed 0.4° C. To compensate for the temperature differences among experiments and to facilitate comparison with estimates of respiration rates of embryos reported in Boehlert et al. (1986), we adjusted the measured rates of oxygen consumption to values at 12.5° C by using a Q_{10} of 1.6. This latter value was chosen because it represents the acclimated Q_{10} value in *S. diploproa* (Boehlert 1978) and such temperature fluctuations are normally experienced by *S. schlegeli* in this season.

Specimens were divided to two groups based upon reproductive status. The first group comprised males, immature females and spent females; the second, females with gestating embryos at different stages of development. The respiration rates as a function of weight for the first group were fitted to a curve, which could then be used to predict normal respiration rates (i.e., for non-gestating fish). Estimates from this curve could then be applied to the second group; the difference between observed and predicted respiration rates was attributed to oxygen consumption by embryos within the ovaries plus associated costs of live-bearing.

Results

Gestating fish with embryos at various stages of development were typically much heavier at a given length than were males (n = 32) and immature or spent females (n = 11). The length-weight curves (Fig. 1) for these groups are as follows:

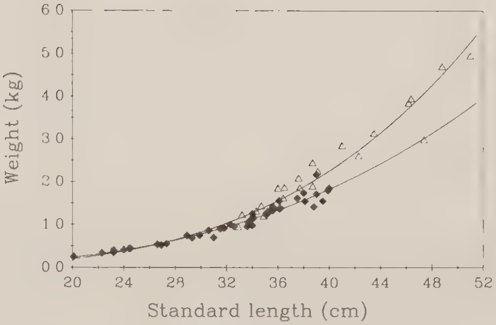

Fig. 1. Length-weight relationships of *Sebastes schlegeli*. The triangles and upper curve represent data from gestating females. Diamonds and the lower curve represent males and immature spent females. The fitted curves (equations 1, 2) are listed in the text.

$$\text{Gestating females: } W = (5.7524 \times 10^{-6})\, L^{3.4910}, \quad n = 25,\ r^2 = 0.937, \tag{1}$$

and

$$\text{Non-gestating fish: } W = (3.3677 \times 10^{-5})\, L^{2.9554}, \quad n = 43,\ r^2 = 0.976. \tag{2}$$

The weight increase of gestating females compared with non-gestating fish was most evident after about 32 cm standard length (SL), and the divergence between the two curves increased with increasing length. This is related to rapidly increasing fecundity with length (Kusakari 1991).

Fish were generally inactive in the respirometers after the first few minutes. In one case, however, considerable activity was observed, and bouts of activity could be seen on the strip chart recording of oxygen consumption. Oxygen consumption rates of this fish were nearly twice that of inactive fish of similar weight and were not used in our analysis.

Oxygen consumption rates were determined for 23 non-gestating fish, including 19 males, 2 immature females and 2 spent females, and also for 17 gestating females with embryos at stages 1 to 30. Respiration rates typically increased with increasing body weight for non-gestating and gestating fish

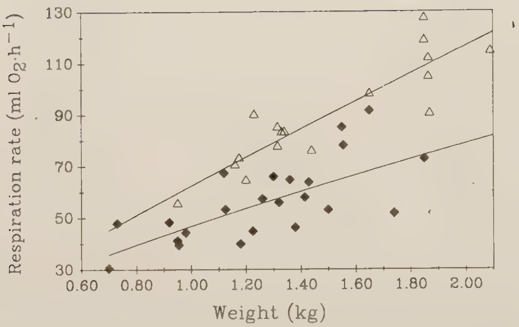

Fig. 2. Oxygen consumption rates as a function of weight for *Sebastes schlegeli*. Triangles represent values from gestating females, and diamonds for males, immature females and spent females. All values are scaled to 12.5° C using a Q_{10} value of 1.6. The corresponding lines representing the fitted curves (equations 3, 4) are in the text.

(Fig. 2). Data from non-gestating fish were fitted to the curve

$$Q = 46.734\ W^{0.7515},\ n = 23,\ r^2 = 0.524, \tag{3}$$

where Q = oxygen consumption rate (ml $0_2 \cdot h^{-1}$) and W = body weight (kg). At a given body weight, respiration rates were much higher for females with developing embryos. Data from these females were fitted to the curve

$$Q = 62.383\ W^{0.9014},\ n = 17,\ r^2 = 0.81. \tag{4}$$

These two curves (Fig. 2) are significantly different (analysis of covariance, $p < 0.01$).

Developmental stage of embryos corresponded to estimates of time since fertilization from 0.01 to 45.3 days (Table 1; birth is estimated to occur at 51.5 days after fertilization). Since respiration rates of embryos increase exponentially with time in *S. schlegeli*, the variability in the respiration rates for gestating females may be partially a result of the variation in the stage of development of embryos in the ovary. Post-fertilization fecundity was estimated and then multiplied by the oxygen consumption rate of embryos at the appropriate stage of development from the equations given in Boehlert et al. (1986). The resulting estimate of the total oxygen consumption rate of embryos in each gestating female was also adjusted to a temperature of 12.5° C

Table 1. Data on respiration rates and embryos of gestating female *Sebastes schlegeli* used in the experiments. All respiration rates are adjusted to a temperature of 12.5° C by using a Q_{10} value of 1.6.

Fish weight (g)	Respiration rate (ml $O_2 \cdot h^{-1}$)	Adjusted respiration rate 1.5 kg fish (ml $O_2 \cdot h^{-1}$)	Excess respiration (ml $O_2 \cdot h^{-1}$)	Time since fertilization (days)	Total embryo respiration rate (ml $O_2 \cdot h^{-1}$)	Live-bearing cost (ml $O_2 \cdot h^{-1}$)
1315	85.56	96.51	39.59	35.50	37.65	1.94
1870	90.87	75.08	18.16	29.80	25.25	− 7.08
1200	64.91	78.91	21.99	35.50	37.65	−15.67
1865	105.08	86.50	29.58	32.60	30.73	− 1.15
1440	76.39	79.17	22.25	35.50	37.65	−15.40
1650	98.54	90.42	33.50	35.50	37.65	− 4.16
1850	119.21	98.31	41.39	38.60	46.80	− 5.41
950	55.90	83.84	26.92	26.20	19.62	7.30
2090	114.88	85.47	28.55	28.20	22.57	5.99
1175	73.48	91.65	34.73	12.60	7.56	27.18
1160	70.93	89.40	32.48	14.40	8.58	23.90
1230	90.47	109.02	52.10	29.80	25.25	26.85
1330	83.55	93.20	36.28	0.01	3.13	33.15
1340	83.68	92.70	35.78	23.70	16.46	19.31
1850	127.80	105.10	48.18	44.60	71.27	−23.10
1315	78.10	87.89	30.97	42.50	61.52	−30.55
1865	112.25	92.15	35.23	45.30	74.86	−39.63

using a Q_{10} of 1.6. The 'non-gestating' weight of the gestating female (estimated from standard length and equation 2) was used to estimate respiration rate from equation 3. Excess respiration rate was determined by subtracting the resulting values from the observed respiration rates. Excess respiration rates were positively correlated with the total oxygen consumption rate for embryos ($r^2 = 0.637$, $p = 0.006$) and can be attributed to the sum of respiration by embryos and live-bearing costs.

To this point, our analysis was confounded by variations in the stage of development and in female size; these variations made it difficult to compare the contribution of the two components of excess respiration (Table 1). For this reason, we adjusted the measured oxygen consumption rates of gestating females, using the weight exponent in equation (4), to a uniform weight of 1.5 kg. This value corresponds to a 35.6 cm SL fish with an estimated post-fertilization fecundity of 126 923 embryos. The associated oxygen requirement of the ovaries varied with the age of the embryos from 3.13 to 74.86 ml $0_2 \cdot h^{-1}$ (Table 1). The same fish in non-gestating condition would have a corresponding weight of 1.3 kg (equation 2) and an estimated respiration rate of 56.92 ml $0_2 \cdot h^{-1}$ (equation 3). The mean excess respiration of these adjusted data is 33.39 ml $0_2 \cdot h^{-1}$. Estimates of live-bearing costs (excess respiration minus respiration rate of embryos) have a negative relationship with the time since fertilization (TSF, in days), as follows:

$$Q_e = 46.533 - 1.5434\ (TSF),$$
$$n = 17,\ r^2 = 0.762, \qquad (5)$$

where Q_e is excess respiration less embryo respiration rate. This relationship suggests that live-bearing costs to gestating females are high early in gestation and decrease to negative values with further development of the embryos (Table 1, Fig. 3). The value approaches zero at about 30 days, which corresponds to a developmental stage of 26.5, near the time when the embryo begins consuming ovarian fluid (Boehlert et al. 1986). This stage is characterized by pigmented eyes with nearly complete lens and fully formed otoliths, rectum and urinary bladder (Yamada & Kusakari 1991).

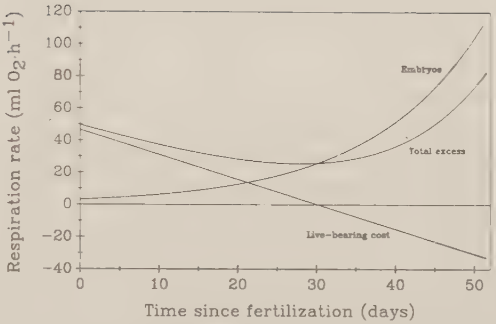

Fig. 3. Dynamics of excess oxygen consumption during gestation for a 1.5 kg gestating female. The respiration of embryos is taken from fecundity multiplied by respiration rate of individual embryos (from Boehlert et al. 1986) and adjusted to a temperature of 12.5° C. The straight line is the estimate of live-bearing cost from equation 5 and Figure 4. The final line represents the sum of these two.

A summary of the proportions of oxygen consumption of a 1.5 kg gestating female *S. schlegeli*, when partitioned to total oxygen consumption of embryos and the live-bearing costs from equation (5), shows a slight dip followed by a rapid rise in total excess respiration rate (Fig. 3). Integrating these functions over the 51.5 days of gestation, one can estimate the total additional oxygen consumed by a 1.5 kg gestating female. Embryo oxygen consumption would require 39 575 ml 0_2, and the live-bearing cost would amount to 8393 ml 0_2. The oxygen consumed by a non-gestating fish over 51.5 days (from integration of equation 3) would be 70 352 ml 0_2. Thus, the total excess respiration represents an increase of 68% of the oxygen necessary for routine respiration over the period of gestation.

Discussion

Within the framework of reproductive effort in fishes, a variety of expenses are incurred. While the major energetic expense of most oviparous fishes is the elaboration of the gonads, selected species develop secondary sexual characters, undergo reproductive migrations and incur various costs associated with some form of parental care (Calow 1985). In livebearers, the costs of protecting the embryos can include additional work for the cardiac system in supplying blood to the ovaries, greater work for the branchial pump, increased costs of osmotic and ionic regulation as more blood passes through the gills and, in some cases, provision of additional nutrition to the embryos (Webb & Brett 1972, Boehlert & Yoklavich 1984). In *S. schlegeli*, significantly greater respiration rates in gestating females suggest a much higher level of energy consumption than in non-gestating fish of equal weight (Fig. 2). These differences are even greater for fish of equal length since gestating fish are heavier at a given length (Fig. 1). Much of this excess oxygen consumption may be consumed by developing embryos, but additional oxygen consumption by the maternal system is also necessary during gestation (Fig. 3).

The reduction of live-bearing costs to values below the estimated respiration rate of the embryos (Fig. 3) occurs about 30 days after fertilization and coincides with developmental stages 26–27. Boehlert et al. (1986) have suggested that respiration rates measured in vitro for embryos may have been slightly inflated for two reasons. First, the rates have been measured in air-saturated saline, whereas the ovarian fluid may have values below saturation. Second, activity by later stage embryos in the respiration flasks may inflate the measured values. The respiration rates may be indirectly estimated if it is assumed that the only source of additional nutrition for embryos comes from resorption of embryos dying early in gestation; that is, from an energy standpoint (but not from exchange of respiratory gases and metabolic waste products), the ovaries are a closed system. This has been hypothesized by Boehlert et al. (1986) and is supported by ingestion of yolk proteins by late stage embryos (K. Takano personal communication). The energy decrease in the ovary during gestation for the 1.5 kg female is about 95.2 kcal. This is based both upon the reduction in fecundity due to unfertilized eggs and death of embryos, and the decreased energy content per embryo (1.48 cal) as compared with a newly fertilized egg (1.59 cal). Partitioned over the surviving embryos, this amounts to about 0.75 cal each, compared with the estimated catabolic utilization of 1.386 cal from Boehlert et al. (1986). If this assumption is correct, the values of in vivo respiration of embryos may be inflated by as much as 85%, and a greater proportion of the excess respiration may be attributed to that needed by the female for the other costs associated with livebearing. A recalculation of the data for the respiration of *S. schlegeli* embryos by using only values for embryos younger than 30 days after fertilization (prior to activity exhibited in the Gilson respirometer flasks) results in an estimated catabolic utilization of about 0.70 cal, which is nearly in agreement with that calculated above.

These data can be used to estimate the costs incurred in reproduction by our hypothetical, 1.5 kg (35.6 cm SL) gestating female. First, the excess oxygen consumption during gestation is represented by the sum of the integrals of the two curves in Figure 3; a total of 47 968 ml 0_2 is consumed above that estimated for normal respiration. This is equivalent to 222.0 kcal based on the oxycalorific conversion of Elliot & Davison (1975). This figure should be reduced by the difference between initial and final energy content of the ovary; the difference is used here as an estimate of the catabolic energy usage and amounts to 95.2 kcal. Thus, the additional cost to the female would be 126.8 kcal. Partitioned among the embryos at parturition, this results in an additional energy commitment by the female of 1.00 cal per embryo. Given that the initial energy content of the egg is 1.59 cal at fertilization (Boehlert et al. 1986), this figure suggests that the energetic cost of livebearing in this species is 62.9% higher than that of oogenesis alone.

That the total 'excess' respiration of females during gestation remains fairly constant (Fig. 3) suggests that some upper limit for oxygen consumption may exist. Metabolic scope may be defined as the difference between the maximum active metabolic rate supportable by aerobic metabolism and standard metabolic rate (Fry 1971); this topic has recently been reviewed by Priede (1985). Activity levels and metabolic scope in fishes are generally related to the gill morphology, particularly some index of gill surface area to body weight (Gray 1954, De Jager & Dekkers 1975); the ability to better extract oxygen from water allows a greater metabolic scope for the more active species (Priede

1985). Benthic species of *Sebastes* such as *S. schlegeli* are not typically highly active fishes and are, in many cases, territorial (Larson 1980). Although the gill surface areas of *Sebastes* species have not been measured, the related scorpaenid *Scorpaena porcus* has a relatively low index for gill area, falling into the same general range of values for other demersal fishes (Pauly 1981). Since gill surface area is typically a function of length, the additional weight added during parturition in female *Sebastes* (Fig. 1) alone will add oxygen demand with the same gill surface area. This will presumably require increased cardiac output under resting conditions. It would be of interest in this context to compare allometric relationships of gill surface area in male and female *Sebastes*, because males might not show such increased respiratory needs.

While the added weight and respiratory demands of developing embryos will contribute to a general decrease in the metabolic scope, other factors must also be considered, including general swimming activity and energy for digestion (specific dynamic action, SDA; Beamish 1974). Vahl & Davenport (1979) have demonstrated an increase of 60% of the metabolic rate in *Blennius pholis* associated with a large ration; they attributed this increase to apparent SDA, suggesting that, in this fish and other species [interpreting data from Muir & Niimi (1972) and Beamish (1974)], a single, large ration may decrease the scope for activity by some 50% for several hours. In *S. schlegeli*, the difference between respiration rates of gestating and non-gestating fish (Fig. 2) increases with increasing length, from 35% for a 30 cm SL fish to 117% for a 50 cm SL fish (Fig. 4). The values for larger fish are significantly in excess of the rates cited for the SDA-mediated increase by Vahl & Davenport (1979). Further, the increases associated with gestation are not transitory, as are those associated with SDA, but last for 51.5 days in *S. schlegeli* (Boehlert et al. 1986). We hypothesize that gestating *Sebastes* may thus attempt to minimize other sources of oxygen uptake.

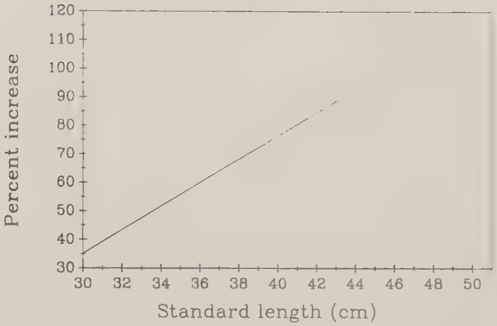

Fig. 4. Increase in oxygen consumption for gestating female *Sebastes schlegeli* as a function of standard length. Values were calculated by first estimating weights from equations (1) and (2) and then determining the respective respiration rates from equations (3) and (4).

Priede (1985) suggested that many fish species must time their feeding activities to keep metabolic rate within the limits of metabolic scope. Over the extended period of gestation, *Sebastes* may need to make accommodations for the reduced metabolic scope associated with the increased respiratory load. Two mechanisms may serve this purpose. First, *Sebastes* females may either feed at lower rations or, later in gestation, cease feeding to minimize the costs of SDA and the swimming activity necessary for feeding. Such cessation of feeding late in gestation has been noted for *S. flavidus* (Eldridge et al. 1991). The energy necessary for maintenance during this period could come from the fat stores accumulated earlier in the season. Guillemot et al. (1985) have noted in five species of *Sebastes* that the accumulation of fat in females is concurrent with gametogenesis and the depletion of fat precedes parturition. Fat is deposited for a longer period and in greater amounts in females than in males. Thus, energy stores may allow a reduced feeding rate and, thereby, a lower SDA component to the reduction of metabolic scope.

A second mechanism to increase overall metabolic scope may be to seek lower temperatures, where tissue metabolism is depressed and oxygen content of the water is greater (Priede 1985). *Sebastes* could conceivably do this in two ways. First, the reproductive season could be timed such that gestation occurs during colder months. Spawning seasonality in some *Sebastes* species occurs throughout the year off the west coast of North America, but the majority of the species spawn in winter and spring months (Parrish et al. 1981). Second, gestating females could migrate to deeper, colder waters. Sexually segregated schools of *S. marinus* and *S. mentella,* for example, exhibit different migration patterns (Sorokin 1961), which may be related to spawning. Gunderson (1971) has noted a similar phenomenon in *S. alutus* and suggested that this species releases larvae in the deepest (and therefore coldest) part of the depth range. Thus, within a season, behavioral thermoregulation may also play a role in the female reproductive process.

The interplay of temperature and oxygen content of water may have impacts on both growth and distribution of *Sebastes*. Boehlert & Kappenman (1980) noted latitudinal trends in growth in two species, with faster growth in the northern parts of the range, where water temperatures are lower and oxygen content higher. Because members of this genus are typically restricted to subarctic and temperate waters (Barsukov 1981), the interplay between temperature and dissolved oxygen may restrict not only the scope for activity and growth of *Sebastes*, but may also make viviparity impractical in lower latitudes from an energetic standpoint. It would thus be interesting to compare the relative temperature-oxygen tolerances of male, non-gestating female and gestating female *Sebastes*. Interannual variability in either food supply or temperature conditions may similarly have large effects on reproduction. Lower food availability in El Niño years, for example, may result in lower fat deposition in *Sebastes* (Lenarz & Echeverria 1986). This may result in either lower somatic growth or reduced fecundity (Wootton 1973). Further, interannual variability in physical conditions may result in variability in the level of nutrition provided to embryos in viviparous fishes (Trexler 1985). The effects of fish size, food availability and physical factors thus have important implications to reproduction in the genus *Sebastes*.

Acknowledgements

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References cited

Amoroso, E.C. 1960. Viviparity in fishes. Symp. Zool. Soc. Lond. 1: 153–181.

Balon, E.K. 1975. Reproductive guilds of fishes: a proposal and definition. J. Fish. Res. Board Can. 32: 821–864.

Barsukov, V.V. 1981. A brief review of the subfamily Sebastinae. J. Ichthyol. 21: 1–26.

Beamish, F.W.H. 1974. Apparent specific dynamic action of largemouth bass, *Micropterus salmoides*. J. Fish. Res. Board Can. 31: 1763–1769.

Berglund, A., G. Rosenqvist & I. Svensson. 1986. Reversed sex roles and parental energy investment in zygotes of two pipefish (Syngnathidae) species. Mar. Ecol. Prog. Ser. 29: 209–215.

Boehlert, G.W. 1978. Changes in the oxygen consumption of prejuvenile rockfish, *Sebastes diploproa*, prior to migration from the surface to deep water. Physiol. Zool. 51: 56–67.

Boehlert, G.W., W.H. Barss & P. Lamberson. 1982. Fecundity of the widow rockfish, *Sebastes entomelas*, off the coast of Oregon. U.S. Fish. Bull. 80: 881–884.

Boehlert, G.W. & R.F. Kappenman. 1980. Variation of growth with latitude in two species of rockfish (*Sebastes pinniger* and *S. diploroa*) from the northeast Pacific Ocean. Mar. Ecol. Prog. Ser. 3: 1–10.

Boehlert, G.W., M. Kusakari, M. Shimizu & J. Yamada. 1986. Energetics during embryonic development in the kurosoi, *Sebastes schlegeli* Hilgendorf. J. Exp. Mar. Biol. Ecol. 101: 239–256.

Boehlert, G.W. & M.M. Yoklavich. 1984. Reproduction, embryonic energetics, and the maternal-fetal relationship in the viviparous genus *Sebastes* (Pisces: Scorpaenidae). Biol. Bull. (Woods Hole) 167: 354–370.

Burggren, W. 1985. Gas exchange, metabolism, and 'ventilation' in gelatinous frog egg masses. Physiol. Zool. 58: 503–514.

Calow, P. 1985. Adaptive aspects of energy allocation. pp. 13–31. *In*: P. Tytler & P. Calow (ed.) Fish Energetics: New Perspectives, Johns Hopkins University Press, Baltimore.

De Jager, S. & W.J. Dekkers. 1975. Relations between gill structure and activity in fish. Neth. J. Zool. 25: 276–308.

Dobbs, G.H. 1975. Scanning electron microscopy of intraovarian embryos of the viviparous teleost *Micrometrus minimus* (Gibbons), (Perciformes: Embiotocidae). J. Fish Biol. 7: 209–214.

Dygert, P.H. & D.R. Gunderson. 1991. Energy utilization by embryos during gestation in viviparous copper rockfish, *Sebastes caurinus*. Env. Biol. Fish. 30: 165–171.

Eldridge, M.B., J.A. Whipple, M.J. Bowers, B.M. Jarvis & J.

Gold. 1991. Reproductive performance of yellowtail rockfish, *Sebastes flavidus*. Env. Biol. Fish. 30: 91–102.

Elliot, J.M. & W. Davison. 1975. Energy equivalents of oxygen consumption in animal energetics. Oecologia 19: 195–202.

Fry, F.E.J. 1971. The effect of environmental factors on the physiology of fish. pp. 1–99. *In*: W.S. Hoar & D.J. Randall (ed.) Fish Physiology, vol. 6, Academic Press, New York.

Gray, I.E. 1954. Comparative study of the gill area of marine fishes. Biol. Bull. (Woods Hole) 107: 219–225.

Guillemot, P.J., R.J. Larson & W.H. Lenarz, 1985. Seasonal cycles of fat and gonad volume in five species of northern California rockfish (Scorpaenidae: *Sebastes*). U.S. Fish. Bull. 83: 299–311.

Gunderson, D. 1971. Reproductive patterns of Pacific ocean perch (*Sebastodes alutus*) off Washington and British Columbia and their relation to bathymetric distribution and seasonal abundance. J. Fish. Res. Board Can. 28: 417–425.

Gunderson, D.R., P. Callahan & B. Goiney. 1980. Maturation and fecundity of four species of *Sebastes*. Mar. Fish. Rev. 42: 74–79.

Kusakari, M. 1978. Mariculture experiments for mass production of juvenile *Sebastes schlegeli*. pp. 117–139. *In*: Annu. Rep. Hokkaido Inst. Mariculture.

Kusakari, M. 1991. Mariculture of kurosoi, *Sebastes schlegeli*. Env. Biol. Fish. 30: 245–251.

Larson, R.J. 1980. Influence of territoriality on adult density in two rockfishes of the genus *Sebastes*. Mar. Biol. (Berl.) 58: 123–132.

Lenarz, W.H. & T.W. Echeverria. 1986. Comparison of visceral fat and gonadal fat volumes of yellowtail rockfish, *Sebastes flavidus*, during a normal year and a year of El Niño conditions. U.S. Fish. Bull. 84: 743–745.

Moser, H.G. 1967a. Reproduction and development of *Sebastodes paucispinis* and comparison with other rockfishes off southern California. Copeia 1967: 773–797.

Moser, H.G. 1967b. Seasonal histological changes in the gonads of *Sebastodes paucispinis* Ayres, an ovoviviparous teleost (Family Scorpaenidae). J. Morph. 123: 329–353.

Muir, B.S. & A.J. Niimi. 1972. Oxygen consumption of the euryhaline fish aholehole (*Kuhlia sandvicensis*) with reference to salinity, swimming, and food consumption. J. Fish. Res. Board Can. 29: 67–77.

Nakanishi, T. 1991. Ontogeny of the immune system in *Sebastiscus marmoratus*: histogenesis of the lymphoid organs and effects of thymectomy. Env. Biol. Fish. 30: 135–145.

Parrish, R.H., C.S. Nelson & A. Bakun. 1981. Transport mechanisms and reproductive success of fishes in the California current. Biol. Oceanogr. 1: 175–203.

Pauly, D. 1981. The relationships between gill surface area and growth performance in fish: a generalization of von Bertalanffy's theory of growth. Meeresforsch. Rep. Mar. Res. 28: 251–282.

Priede, I.G. 1985. Metabolic scope in fishes. pp. 33–64. *In*: P. Tytler & P. Calow (ed.) Fish Energetics: New Perspectives, Johns Hopkins University Press, Baltimore.

Sorokin, V.P. 1961. The redfish: gametogenesis and migrations of the *Sebastes marinus* (L.) and *Sebastes mentella* Travin. Rapp. P. -V. Reun. Cons. Int. Explor. Mer 150: 245–250.

Trexler, J.C. 1985. Variation in the degree of viviparity in the sailfin molly, *Poecilia latipinna*. Copeia 1985: 999–1004.

Vahl, O. & J. Davenport. 1979. Apparent specific dynamic action of food in the fish *Blennius pholis*. Mar. Ecol. Prog. Ser. 1: 109–113.

Ware, D.M. 1975. Relation between egg size, growth, and natural mortality of larval fish. J. Fish. Res. Board Can. 32: 2503–2512.

Webb, P.W. & J.R. Brett. 1972. Oxygen consumption of embryos and parents, and oxygen transfer characteristics within the ovary of two species of viviparous seaperch, *Rhacochilus vacca* and *Embiotoca lateralis*. J. Fish. Res. Board Can. 29: 1543–1553.

Wootton, R.J. 1973. The effect of size of food ration on egg production in the female three-spined stickleback, *Gasterosteus aculeatus*. J. Fish Biol. 5: 89–96.

Wootton, R.J. 1985. Energetics of reproduction. pp. 231–254. *In*: P. Tytler & P. Calow (ed.) Fish Energetics: New Perspectives, Johns Hopkins University Press, Baltimore.

Yamada, J. & M. Kusakari. 1991. Staging and the time course of embryonic development in kurosoi, *Sebastes schlegeli*. Env. Biol. Fish. 30: 103–110.

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A summary of the symposium on rockfishes and recommendations for future research

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Significant progress in our understanding of the reproduction and aspects of the early life history of *Sebastes* was evident in the papers presented at this symposium (not all published in this volume). On the final day, we presented short summaries of this progress made in the various research topics – reproduction, embryonic and larval development, early life history, ecology, mariculture and fisheries applications – and considered the questions and discussions raised during the symposium for further research. A discussion session followed. This paper presents the summaries and, to the extent possible, incorporates points made during the discussion session.

Reproduction

The papers on reproductive biology encompassed several levels of biological organization, including biochemical endocrinology, cellular aspects, development and behavioral ecology of reproduction. New scientific approaches and techniques and integration of established techniques combined to demonstrate common patterns in rockfishes as well as species-specific differences among the different levels of organization. The paper of Akihiko Shinomiya elegantly described, for the first time, courtship and copulatory behavior in *S. inermis* and *Sebastiscus marmoratus* and included underwater video recordings. Courtship and copulation occur at dusk, but mating behavior and seasonality differ between the two genera. During courtship, males exhibit territorial behavior not evident in other seasons; females copulate with more than one male. Future research should extend these studies to other species, especially those occupying different habitats (e.g., pelagic and deepwater species). The possible role of pheromones in reproduction should be investigated. In view of the taxonomic significance of the extrinsic swim bladder muscles, it would be interesting to determine whether they are used to produce unique, species-specific sounds during courtship and mating.

Hiroya Takahashi described histological methods used to analyze the stages in the male and female reproductive cycles of *Sebastes taczanowskii*. Comparison of the reproductive cycles in five other species of *Sebastes* suggests that gametogenesis in both sexes is prolonged in northern species and shortened in southern species. There are several obvious areas for future inquiry, including the physiology of sperm storage, competition from sperm derived from different males and the timing and mechanism of egg fertilization. Papers on endocrinological studies of the reproductive cycle followed. Yoshitaka Nagahama described changes in steroid hormone levels during the reproductive cycles of female *S. taczanowskii* and *S. schlegeli*, giving the first comprehensive description of the endocrinology of the female reproductive cycle in viviparous teleosts. Estradiol-17β is the most important steroid involved in vitellogenesis, and 17α, 20β-dihydroxy-4-pregnen-3-one plays an important role in final oocyte maturation and the maintenance of gestation, but progesterone apparently does not play a significant role. Kazunori Takano described steroid hormone levels in female *Sebastiscus marmoratus*, a rockfish with multiple broods. Changes in hormone levels could be correlated with histological changes in the gonadal cycle, and the roles played by the hormones are similar to those in *Sebastes*. The two studies indicate that there is a commonality in the hormonal control of reproduction in viviparous rockfishes.

Akihiro Takemura described research on female-specific serum proteins (FSSPs) in *S. taczanowskii* using immunochemical procedures. The three FSSPs detected (two of which were categorized as vitellogenin) were utilized during oogenesis. Since the vitellogenin level was low during gestation, two of the FSSPs did not serve as a supplemental source of nutrients for developing embryos. The third FSSP was a major constituent of the ovarian fluid but not of the vitellogenic oocytes, and may play a role in gestation. Comparative studies of seven rockfishes in the genus *Sebastes* and *Sebastiscus* revealed the ubiquity of vitellogenin, whereas the third FSSP was absent in several species of *Sebastes*.

A series of six papers was then presented on the physiological ecology of reproduction and reproductive physiology and development. Ralph Larson discussed the relationship between seasonal cycles of reproduction and of deposition and utilization of metabolic reserves. Compared to most other ectothermic vertebrates, *Sebastes* seems anomalous because some of its species deposit reserves during the period of gametogenesis. Reserve deposition is evident in liver weight and as fat storage in the mesenteries. Reserves decline during winter, coinciding with the main period of reproductive activity – a result suggesting reserves are used in gametogenesis and also for survival during winter when food availability is low. A comparison of northern and southern species reveals interspecific difference in reserves that may be related to geographical differences in the seasonal abundance of food. Further research on this topic should consider timing of the reproductive cycle in terms of the availability of food both for the reproductive adults and the newborn young.

Tina Wyllie Echeverria discussed sexual dimorphism and its causal factors among 34 species of rockfishes. The level of dimorphism varied among species and species groups. Semipelagic species are generally more dimorphic than benthic species in size as well as morphometric measurements. These dimorphisms may reflect compensation in feeding ability in response to reduced size (i.e., larger pectoral fins and eyes could aid males in competing for food) and may be related to mating behavior (larger fin size and head parts). Research to understand the causal basis of sexual dimorphisms would be fruitful. Differences between the sexes in the energetic requirements of reproduction may be related to the dimorphisms.

George Boehlert described research on the physiological energy costs of livebearing to the gravid female as measured by oxygen consumption of the females and the developing embryos. The major cost of livebearing to the gravid female is the energy expended to maintain the environment of the developing embryos, and the metabolic costs apparently are high. It was suggested that the gravid females respond to the increased energetic demands of gestation and reduce their overall metabolism either by decreasing feeding or by seeking lower temperatures. Both hypotheses can and should be tested. The temperature hypothesis is particularly intriguing because it suggests that viviparity with very large brood size is impractical in tropical and subtropical waters, and hence could explain the absence of *Sebastes* from those geographical regions.

Maxwell Eldridge characterized the annual reproductive cycle of the yellowtail rockfish, *S. flavidus*, at different levels of organization, ranging from the community-population level to the subcellular level. The reproductive profile of a southern population differed significantly from that of northern populations. The former population exhibited an annual reversal in sex ratio not previously observed in rockfish. Although the gonadosomatic index accurately profiled the seasonal reproductive cycle for both sexes and proved useful in separating immature from mature fish, it was not as sensitive as histological analysis of the gonads. The experimental program used in this paper provides a comprehensive method for comparing the reproductive profiles of different populations of the same species and the profiles of different species.

Lewis Haldorson reviewed published reports for data describing fecundity, maturity, growth and weight in 54 species in the genus *Sebastes*. Information on maturity and fecundity was examined for patterns associated with taxonomic relationships; this approach allows analysis of rockfish reproduction in the context of life history models. Rockfishes display a great range in size at maturity (9–52 cm), and maximum fecundity can attain a value of 5.60×10^6. Comparisons of exploited and non-exploited populations of rockfish may provide the means for testing various life history models, as elaborated in the later presentation by Bruce Leaman.

John Wourms reviewed viviparity in fishes, gave an overview of selected aspects of rockfish reproduction and development and speculated on the evolutionary origin of viviparity in rockfishes. Among the eight subfamilies of the Scorpaenidae, viviparity is confined to the subfamily Sebastinae; gestation is lumenal and the embryos usually develop to term within the egg envelope. Transitional states from oviparity to viviparity are evident in different species within the family. Although viviparity is best developed in the genus *Sebastes*, it is still primitive and unspecialized. Rockfish viviparity is essentially lecithotrophic (i.e., embryonic nutrition is dependent on the energy reserves laid down during oogenesis). In other groups of viviparous fishes, lecithotrophy has been shown to be better suited energetically to seasonally unpredictable habitats, whereas matrotrophy requires a predictable food supply. During the evolution of viviparity in rockfishes, the advantages of high fecundity associated with oviparity were retained while an enormous increase in the survival rate of the developing embryos was acquired. The basic lecithotrophic pattern of oviparous development did not change since it offered selective advantages both in terms of energetics and as a basis for retaining a large brood size. Comparative studies on reproduction and development of the less well-known sebastine genera *Hozukius* and *Helicolenus* would be beneficial to our understanding of the evolution of viviparity in this group.

Functional aspects of embryos and larvae

Against the rather comprehensive background of reproduction in adults presented in the first section, the second section dealt with various aspects of embryonic and larval development. The papers ranged from descriptive to experimental and demonstrated how the integration of reproductive functions of the female serves to promote internal development of fertilized eggs and embryos through to parturition. The lack of an accurate description of development of *Sebastes* embryos has impeded research comparing development in different species. Livebearing precludes continual observation of the normal developmental events in an individual embryo and prolonged in vitro observation may result in changes from the in vivo pattern (Triplett 1960). Past researchers have either used a modification of commonly used developmental schemes for oviparous fishes or, in at least one case, have developed a new, less detailed scheme specific to *Sebastes* (Stahl-Johnson 1984). Juro Yamada described development in *S. schlegeli* using the former approach. This staging system should serve to improve communication among researchers in *Sebastes* intent on relating results among different species and different laboratories. It can also serve as a point of departure for future studies on the structural aspects of development in *Sebastes*; highly detailed descriptions of structural development of *Sebastes* embryos would be useful to relate to the functional features described for embryos in several papers. Comparative studies with development of *Hozukius*, *Helicolenus*, and *Sebastiscus* could also aid in understanding the evolution of viviparity within the Scorpaenidae.

Yamada also described a technique refining the methodology for determining gestation period, using a great deal of data from *S. schlegeli* from a mariculture laboratory in Japan. This approach appears to be a marked improvement over earlier estimation techniques and produced different results. Boehlert et al. (1986) suggested that the gestation period for this species was 51.5 days, whereas the new technique provides an estimate some 8 days shorter. It is interesting to note that the revised estimate would decrease the catabolic energy consumed, a concern noted in the paper by Boehlert, Kusakari and Yamada and also in the presentation by Boehlert on embryonic energetics.

Frank Conte outlined the ontogeny of the 'sodium pump' in developing embryos and demonstrated their ability to osmoregulate. The titer of the enzyme in embryos of both *S. schlegeli* and *S. taczanowskii* indicated that significant enzyme activity was not present until near stage 18, in general agreement with the results of incubations with saline containing the inhibitor ouabain. One might question the need for osmoregulation by embryos in the benign ovarian environment, since presumably the female can osmoregulate for the embryos and embryos are unable to osmoregulate for long in vitro. In the ensuing discussion, Teruyuki Nakanishi noted that rearing efforts for several species of marine fish larvae in Japan have benefited from using diluted seawater. Rearing trials at salinities 60–70% that of full strength seawater resulted in significantly higher survival rates than in full strength seawater. It is possible that the energetic costs of osmotic and ionic regulation may be put to use for other metabolic purposes during this period of rapid growth.

Boehlert described past work on embryonic energetics, comparing the results from species studied to date. The presentation and ensuing discussion raised several questions. There was some concern over the true rate of respiration of embryos; Conte suggested that incubation with curare in vitro would minimize the muscular activity in the later stages to provide estimates of resting metabolic rate. The question of oxygen tension in the ovarian fluid and the rate of passage through the larger ovaries of some species is also pertinent here. Given that developmental rates are very slow compared to oviparous fishes with similar egg sizes, the control of developmental rates of embryos would be interesting to study. Possible candidates include oxygen delivery by the female system or some level of hormonal control. A simple experiment was suggested in which embryos would be incubated in physiological saline in vitro and the developmental rate at different stages compared with in vivo rates. This has been done with embiotocid embryos by Triplett (1960), who observed earlier loss of spatulate fins and metamorphosis in vitro. He raised the question of potential hormonal involvement in the maternal-fetal relationship. Possible endocrinological links or other chemical communication is unknown in *Sebastes*, but the approach of Nagahama, Takano and their coworkers may answer many questions. Such a study could also address the question of a signal that embryos are ready for birth, if one exists. Finally, this paper pointed out the need for studies on pre- and postfertilization fecundity: are there atretic eggs from unfertilized ova or simply such are the result of embryo death? Eldridge's paper suggested no difference between pre- and postfertilization fecundity in *S. flavidus*, whereas Kusakari documented such a change in *S. schlegeli*.

The two papers on nutritional uptake by embryos took different approaches but reached similar conclusions. The radiochemical approach described by Mary Yoklavich suggests uptake of exogenous substrata at all stages examined, but utilization only in late stage embryos after the point of gut development. Results from autoradiography unfortunately were not consistent. Although a site of uptake could not be traced to the ultrastructural level, histological examination did suggest some epidermal uptake in an early embryo. This was confirmed in several embryo stages in the paper presented by Motohiro Shimizu, who used ruthenium red to demonstrate uptake in the epidermis. Given that the radiochemical results with an amino acid do not support utilization of exogenous substances in the early stages, one might question whether this uptake is nutritionally meaningful. The hindgut is clearly the site of pinocytotic uptake of substances. After the mouth opens, ingestion of ovarian fluid results in uptake in the hindgut, which is morphologically similar to that in other feeding fish larvae. Further research will be necessary to identify the source of the exogenous substances consumed: are they intraovarian or supplied from the maternal system? The approach of Takemura and his colleagues could be supplemented by a radiochemical study with peptides or proteins of different molecular weight to address this question. The final histological question identified as needing more research was on the function of sacciform cells. As demonstrated by Shimizu, the sacciform cells are highly abundant, but their function remains unknown (Bullock 1980). They appear, however, not to be absorptive.

Nakanishi described work on the development of the immune system in *Sebastiscus marmoratus* larvae. Again, the issues of the generic identity and the relationship of *Sebastiscus* and *Sebastes* were raised, making comparative work with the latter genus of interest. Nakanishi's approach provides encouragement for further research on the development of organ systems not only in larvae but in embryos as well. The late elaboration of the lymphoid system in *Sebastiscus marmoratus* again raises the question of hormonal control of organogenesis in embryos. In the case of the lymphoid system, however, it is not under maternal control, because development does not occur until well after parturition.

Identification, systematics and ecology

The presentations by Arthur Kendall and Lisa Seeb showed that the last few years have seen major advances in the identification of *Sebastes* larvae and juveniles. These advances have come from two very different directions. One is the traditional methodology utilizing superficial morphological characters. While a number of *Sebastes* larvae may now be identified through examination of cranial spines, pigment spots and other characteristics, the limits to the utility of this approach may be near. It is quite possible that a number of closely related species may not be distinguishable using this protocol. Seeb's presentation takes us to the next step, the use of molecular techniques such as allozyme analysis and mitochondrial (mtDNA) and nuclear DNA restriction fragment polymorphism analyses. However, the usefulness of these more esoteric techniques will depend on several factors. Perhaps the most important is a data base developed for adult *Sebastes* that will allow identification of larvae and juveniles. Second, the laboratory techniques needed for these methods have not yet been fully codified.

Research on *Sebastes* systematics, an area given little attention in recent years, is approached in several imaginative ways. Kendall shows that rockfish larvae and juveniles may be characterized using various morphological characters. These species may also be grouped by these characters, and these groups compared with currently accepted subgeneric alignments. This technique met with only limited success, indicating that some subgenera are probably artificial species groups with convergent morphologies.

In reference to Seeb and Kendall's paper, DNA techniques for research on *Sebastes* systematics point the way to the future in this field. Indeed, the great sensitivity of various DNA techniques (such as mtDNA and nuclear DNA restriction fragment polymorphisms) may prove to be a two-edged sword. For instance, Seeb mentioned the difficulties in distinguishing the putative sibling species *S. carnatus* and *S. chrysomelas*, even with mtDNA analysis, thereby implying greater complexity in rockfish systematics. The application of DNA techniques to systematics research may therefore force the use of other methods, such as crossbreeding, to sort out relationships.

Geoffrey Moser presented a wealth of information on distribution and seasonality of *Sebastes* larvae off California and Baja California. His paper is a badly needed synthesis of an important time series of data and will help us in understanding the distribution patterns of larvae. Still needed, however, are further explanations for some of these patterns, particularly those environmental factors that contribute to annual variation in larval incidence and abundance. Better taxonomic resolution will be necessary to provide much of this analysis.

Moser also discussed the pelagic juvenile interval of *Sebastes*, summarizing work that represents a major advance in our understanding of an area for which relatively little data were previously available. However, as with the larval stages, a number of questions remain. Among these are the factors leading to enhanced juvenile survival and how these young fish find suitable habitat for recruitment. Indeed, the question of rockfish navigation remains something of a mystery.

Milton Love focused on juvenile *Sebastes* ecology. Recent research has given us a much better idea of the recruitment patterns of shallow-water *Sebastes*. New data are available on annual variability in inter- and intraspecific recruitment magnitude. Recruitment variation now appears to be strongly influenced by pelagic juvenile availability. Algae and other attached macrophytes play an important role in the recruitment process. However, whether these plants are essential for these recruits is not known. Algal removal experiments would be a natural follow up.

Various types of movements have recently been examined. Of particular interest are the ontogenetic shifts of newly recruited juveniles from *Macrocystis* and *Nereocystis* canopies down to understory benthic algae. Considerable data indicate that seasonal movements occur. Storm-derived turbulence, in particular, may drive young-of-the-year rockfish from nearshore habitats, though their destination is unclear. Increasing attention has been focused on diel movements, and indications are that these movements are complex, with activity patterns changing as the young-of-the-year mature.

The role of the large schools of juvenile rockfish in kelp beds in regulating invertebrate populations through predation on larvae has been given some attention, but pertinent experiments have not been done. For instance, it would be a simple matter to measure plankton entering and exiting a kelp bed during daylight hours when rockfish are most actively feeding, and at night when predation is reduced.

Lastly, virtually no information is available on the ecology of deepwater juvenile *Sebastes*. It is hoped that directed research with remotely operated vehicles and manned submersibles will make greater advances in this area.

Mariculture and fisheries

In order to enhance depleted stocks of *Sebastes*, three major aspects must be considered. First, improvement of mariculture technology is necessary to raise large numbers of juveniles as efficiently as possible. Second, ecological evaluation of the effects of releases of cultured juveniles on stocking and fishery yield must be considered. Third, in connection with the second, is the justification and selection of target species based upon life history and economic grounds.

The current status of technology for mariculture of *S. schlegeli* as developed in Hokkaido, Japan, was presented by Kusakari, who showed that rearing of larvae up to 10 cm juveniles can be attained with relatively low mortality on the order of 45%. Major problems in this process are diseases causing mortality. Studies of immune systems during ontogeny, as described in *Sebastiscus marmoratus* by Nakanishi, will be needed for more effective culture of juveniles. The possibility of endocrinological control of reproduction should be examined for improvement of brood stock management and collection of larvae. In this connection, it is important to identify the hormones involved in the maturation of gonads, mating behavior, internal fertilization, maintenance of gestation and parturition. This approach should be encouraged by the results presented by Nagahama and Takano. Seasonal cycles of reproduction in various species were addressed by several authors; changes of energy reserves by Larson, comprehensive analysis of reproductive performance by Eldridge, female-specific serum proteins by Takemura, gonad maturation by Takahashi and Takano, all are important factors for brood stock management. Developmental stage analysis and the time course of embryonic development, beyond that tentatively presented by Yamada, are also essential knowledge for aquaculture.

The theoretical effects of releasing hatchery raised juveniles on stock of *Sebastes alutus* were described by Jeffrey Polovina. Based on a simulation using the Deriso-Schnute model, he proposed that hatchery releases can potentially restore a depleted population and may be economically feasible if juveniles are raised at a cost below US $ 0.15 per individual. Kusakari commented that the present cost for raising one 10 cm juvenile *S. schlegeli* is 70 yen (equivalent to US $ 0.50), but this cost can be reduced if the economics of scale are achieved as in the case of *Paralichthys olivaceus* now being produced on a large scale in Japan. Culture of larvae to juveniles of an optimal size implies lowering the natural mortality in the early life stages by protecting them from predation with a sufficient supply of prey. Release of cultured juveniles, therefore, can cause changes in the ecological traits of a population through a density change. Leaman discussed compensatory responses to exploitation of *Sebastes* populations based on life history theory as applied to *S. alutus*. Impacts of increased recruitment through stocking can be analyzed on the same basis, but as the reverse of exploitation. Long-term analyses of tagging and recapture experiments of released fish are necessary.

In Japan, the mariculture project started without much knowledge of life history and ecology of each target species. Some coastal species of *Sebastes* and *Sebastiscus* were considered to be best suited to mariculture because of their peculiar mode of reproduction, high fecundity and presumed nonmigratory behavior. These criteria should be reexamined in light of Leaman's analyses, in which *Sebastes* species were characterized as iteroparous long-lived fishes.

In the ensuing discussion session, one of the most lively topics was why North Americans have been unable to rear *Sebastes* with the success of the Japanese. Mortality rates in studies in the United States have been extremely high compared to Japanese efforts, with few, if any, juveniles reaching ages in excess of 50 days (Fig. 1). Several reasons were offered, including the smaller larvae in the eastern Pacific, the lack of sophisticated food rearing capabilities and the frequent use of embryos that were artificially extruded. On the latter point, the importance of using embryos born naturally to females after carrying them through the full term of gestation was noted. It was concluded that there is no a priori biological reason for this problem, but rather that it is a technological one; rearing attempts in the United States have often been on an ad hoc basis and not with funding dedicated for the purpose. Although the larvae are significantly smaller, this has not impeded complete rearing of larvae of other fishes.

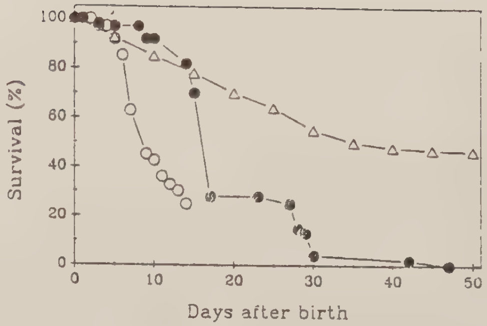

Fig. 1. Survival rates of *Sebastes* larvae in rearing trials, comparing efforts in the United States and Japan. Triangles, *S. schlegeli* (Kusakari this volume); filled circles, *S. melanops* (Boehlert & Yoklavich unpublished data); open circles, *S. auriculatus* (Stahl-Johnson 1984).

Considerable discussion also occurred on the importance of further research and the factors impeding research progress. Availability of funding was a real concern. It was recommended that U.S. investigators and the agencies that support their work incorporate the experimental, laboratory-based approach into the investigation of the biology of fishes. There is need for basic research in morphology, physiology, genetics, life history, development and cell biology both in rockfishes and fishes in general.

For many reasons, the study of fish reproduction and the development of viviparous fishes such as rockfishes is both important and interesting. First, fishes are the most abundant, most diverse and yet the least known group of vertebrates. Second, fishes are the most primitive vertebrates and include the lineage from which tetrapods, including mammals and man, evolved. Accordingly, they are excellent models for elucidating the origins of vertebrate developmental mechanisms. Third, as a diverse group, fishes exhibit a diversity of developmental patterns, so that it is possible to find a 'system' that will be applicable to many problems. Fourth, our current knowledge of vertebrate development is actually very poor, because it is based on a very small and biased sample. Finally, fishes as a group are of major economic importance. With the decline in populations of wild stock and the increase in number of species used in aquaculture and mariculture, intensive study of fish reproduction and development becomes imperative if these enterprises are to succeed. Many of the same arguments used to justify the study of fish development in general can be extended to the development of viviparous fishes including rockfishes. Several additional features should also be considered. Viviparity makes its first appearance in the vertebrates among fishes. Viviparity has repeatedly and independently evolved from oviparity among fishes. The evolution of vertebrate viviparity led to the establishment of specialized maternal-fetal relationships. Nearly all of the adaptations for viviparity that occur in higher vertebrates, including mammals, first appear in fishes. Fishes also possess unique adaptations.

Epilogue

The papers presented at this symposium have increased the level of our knowledge on the reproduction and early life history in the genus *Sebastes* and have developed new techniques and approaches. As is characteristic of good research on new problems, however, the papers raise more questions than they answer. We hope that future collaboration and cooperation will be fostered by this meeting and the publication of the proceedings and will result in an effort to develop research to address the questions.

References cited

Boehlert, G.W., M. Kusakari, M. Shimizu & J. Yamada. 1986. Energetics during embryonic development in the kurosoi, *Sebastes schlegeli* Hilgendorf. J. Exp. Mar. Biol. Ecol. 101: 239–256.

Bullock, A.M. 1980. A comparative study of the epidermal morphology of fishes of the order Anacanthini with reference to their ecology and distribution. Oceanogr. Mar. Biol. Annu. Rev. 18: 251–315.

Stahl-Johnson, K.L. 1984. Rearing and development of larval *Sebastes caurinus* (copper rockfish) and *S. auriculatus* (brown rockfish) from the northeastern Pacific. M.S. Thesis, University of Washington, Seattle. 217 pp.

Triplett, E.L. 1960. Notes on the life history of the barred surfperch, *Amphistichus argenteus* Agassiz, and a technique for culturing embiotocid embryos. Calif. Fish Game 46: 433–439.

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Introduction to the symposium on rockfishes

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The genus *Sebastes* is derived from a predominantly tropical family, yet represents an important component of shelf and slope fish faunas of temperate and subarctic regions. Although ecologically important in many habitats, most *Sebastes* spp. have reproductive and early life history features that are rather poorly understood. Understanding the dynamics of the reproductive process and the ecology of early life history stages is essential to knowledge of fisheries exploitation, stock dynamics and aquaculture. Recent research on the genus has modified our thinking about reproduction, particularly related to energetics and mechanisms involved in the live-bearing mode of reproduction. Equally significant advances have been made in our understanding of the early life history of many species.

This publication is the result of a seminar entitled 'Rockfishes of the genus *Sebastes*: their reproduction and early life history' convened to bring together scientists interested in these topics and to share the different scientific approaches taken in North America and Japan. In this introduction, we make some brief comments on the genus and describe the development of the different research approaches.

The ecological importance of *Sebastes* is evident from its speciose nature. With a center of distribution in the North Pacific, this genus has the greatest diversity on the west coast of North America (about 69 species), followed by the waters of Japan and south to Taiwan (about 32 species), the North Atlantic (some 4 species), and in the Southern Hemisphere (at least 1 species). Species range from small, short-lived shallow-water fishes, such as *S. emphaeus* (Moulton 1975), to large, long-lived, very abundant, shoaling fishes such as *S. marinus*, *S. alutus* and *S. entomelas*. These latter species are commercially exploited, but fisheries for *Sebastes* have not typically been success stories: worldwide catch declined from 768,481 metric tons (t) in 1976 to 483,733 t in 1986 (FAO 1977, 1988). During this time interval, the U.S. catch decreased from 17,144 to 10,325 t and the Japanese catch decreased from 54,310 to 2006 t. A dramatic case in stock decline is that of the Pacific ocean perch, *S. alutus*, for which biomass estimates of the west coast stock decreased from 144,000 to 13,500 t from 1958 to 1975 (Ito et al. 1987). The decline of catch in the northeast Pacific is now well documented (Bracken 1987), as are declines in biomass of northwest Atlantic species. The alarming reduction in the Japanese catch, combined with increased interest in coastal fisheries after the establishment of 200 mi exclusive economic zones in the mid-1970s, prompted aquaculture research on *Sebastes* with the goal of releasing hatchery-raised juveniles to enhance depleted stocks in coastal waters (Sakai et al. 1985). In the United States and Canada, by contrast, management measures, often including closure of fisheries, have been instituted (Gunderson 1984). There are clearly concerns by U.S. and Japanese scientists, among others, about the status of *Sebastes* stocks.

Diversity in reproductive biology characterizes the family Scorpaenidae, which has some 60 genera and 330 species in 8 subfamilies. Many of the subfamilies are distributed in tropical and subtropical regions from deep to shallow waters. Seven of the subfamilies are characterized by a strictly oviparous reproductive mode, with external fertilization and development of eggs. In the Sebastinae, however, internal fertilization seems to be the rule. This subfamily has been reviewed by Barsukov (1981), and his system of phylogeny, although disputed by many taxonomists, clearly demonstrates the complexity of the subfamily. Four genera are typically recognized, with 2 species of the most primitive (and poorly known) *Hozukius,* 13 of *Helicolenus,* 3 of *Sebastiscus,* and approximately 103 of *Sebastes*. *Sebastiscus* has been called a subgenus of *Sebastes* by Barsukov & Chen (1978), but most continue to recognize it as a genus. *Sebastes* seems to be the most highly derived genus in the subfamily, if not in the family, from both evolutionary and reproductive standpoints.

The reproductive mode in *Sebastes* has in the past been characterized as unspecialized lecithotrophic viviparity (ovoviviparity). After mating and copulation, fertilization occurs within the ovary; embryos are brooded for approximately 1 month, and birth (also referred to herein as either spawning or parturition) occurs with the release of relatively undeveloped embryos or larvae, 3–9 mm long. The contrast with matrotrophic viviparity, wherein the embryos receive additional nutrition during gestation, has been questioned by recent research (Shimizu & Yamada 1980, Boehlert & Yoklavich 1984, Boehlert et al. 1986). Nutritional relationships of embryos are of great evolutionary significance and have an important bearing upon our understanding of reproduction in fishes. There are further implications, moreover, for questions of fishery management (Garrod & Horwood 1984), because reproductive energy costs in this genus may be higher than previously thought.

Variability in reproduction may lead to implications for survival at the early life history stages as well. *Sebastes flavidus* appears to deposit less lipid energy reserves in El Niño years (Lenarz & Echeverria 1986); this could conceivably lead to either reduced fecundity or less fit larvae. After parturition, early life history stages of *Sebastes* are planktonic, in some cases in excess of 1 year. The effects of environmental variation on reproduction and the role of the maternal system in post-parturition survival is thus an important concern.

An intimate knowledge of the reproductive process is required for aquaculture of any species, both for brood stock management and rearing of larvae. Similarly, knowledge of early life history and ecology is important, especially when juveniles are released to the wild, as in stock enhancement. Lack of such knowledge may have impeded early attempts at enhancement of cod stocks in the United States and Europe (Shelbourne 1964). High densities, for example, can lead to increased aggression in territorial species of *Sebastes* (Hoelzer 1987). Combined knowledge of reproduction and early life history can increase capabilities in the areas of both fisheries and aquaculture.

Studies on reproductive biology and early life history of *Sebastes* have been conducted for many years in both the United States and Japan, but the motivations for the studies differed somewhat and thus led to different approaches. For both countries, the importance of *Sebastes* in marine fisheries served a major role in stimulating research. The secondary motivations, however, relate to aquaculture potential in Japan and basic ecology pertinent to fisheries management in the United States. The two countries also have different approaches to coastal marine fisheries resources; Japan has developed an energetic aquaculture industry to replenish coastal resources while the United States has concentrated on natural production and management of stocks. An examination of pertinent publications demonstrates the differences between research approaches in Japan and North America (the United States and Canada). Research papers on *Sebastes* in North America have been dominated by the topics of biology, systematics, fisheries and ecology and, to a lesser extent reproduction, physiology and food science (Fig. 1a). Japanese publications, on the other hand, have been dominated by reproduction, physiology, biology, systematics and, to a lesser extent, aquaculture, ecology and fisheries. In North America, early research was principally on systematics and basic biology, whereas studies in fisheries and ecology have increased over recent decades (Fig. 1b). A major goal of the seminar on reproduction and ecology of early life history in *Sebastes* was to join the separate strengths of U.S. and Japanese investigators.

The role of fisheries in research on *Sebastes* in North America began on the east coast, where depleted stocks of redfish, *S. marinus,* led to convening one of the first international symposia on the genus (Trout 1961). As west coast fisheries on rockfish took on increasing importance, directed fisheries research on *Sebastes* developed (Phillips 1964). The abundance of larvae was recognized as important from early studies of the California Cooperative Oceanic Fisheries Investigations (Ahlstrom 1961). Ecological studies arose from the many species of *Sebastes* and their importance in coastal ecosystems, particularly on the west coast, resulting in studies on all phases of the life history: ecology of pelagic larvae and juveniles (Ahlstrom 1961, Moser & Ahlstrom 1978), reproduction (Moser 1967, Boehlert & Yoklavich 1984), behavior and ecology of adults (Larson 1980) and ecology and energetics of benthic juveniles (Boehlert & Yoklavich 1983). The importance of many species to fisheries and the effects of declining stocks also prompted research (Gunderson & Sample 1980) and attempts to understand recruitment dynamics (Mearns et al. 1980, Norton 1987). Interest in the genus thus continues.

In Japan, the commercial importance and peculiar reproductive features of *Sebastes* and *Sebastiscus* attracted the interest of many investigators. Earlier studies were conducted with some commercially important species on development of embryos and larvae (Fujita 1957, Shiokawa & Tsukahara 1961), age, growth and maturation (Mizue 1957, Harada 1962), reproductive cycles including gametogenesis (Igarashi 1968) and larvae and juveniles (Sasaki 1976, Hoshiai 1977). After the depletion of coastal stocks of rockfishes became apparent, efforts were first directed to construction of artificial shelters for restocking coastal species, based on their ecological and behavioral characteristics in relation to their habitats (Hatanaka & Iizuka 1962, Yamagishi et al. 1984). Establishment of 200 mi economic zones in the late 1970s pushed the Japanese fisheries administration to take more active measures; that is, aquaculture production of young fish to be released into the open sea was encouraged. The main target species were *Sebastes schlegeli* and *Sebastiscus marmoratus,* with *Sebastes thompsoni* and *S. inermis* in some local areas. Much of the early research on *S. schlegeli* was done at the Hokkaido Institute of Mariculture (Kusakari et al. 1977), and further research activities extended to other laboratories (Ikehara et al. 1980). The aquaculture of *Sebastiscus marmoratus* was developed in southern prefectures (Ohgami et al. 1979). Based largely on materials available from aquaculture facilities were studies on the reproductive mode (Ouchi et al. 1978, Takemura et al. 1989), ultrastructure of embryos (Shimizu & Ya-

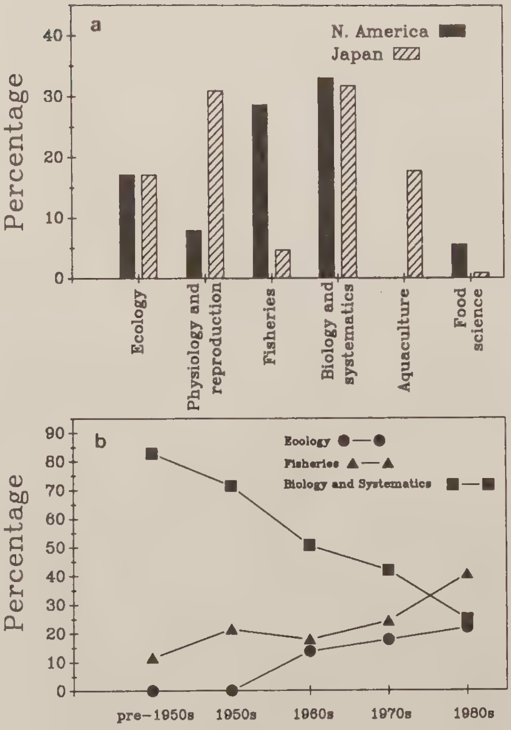

Fig. 1. (a) Differences in research effort on *Sebastes* in North America and Japan as shown by publications, and (b) changes in the disciplinary research effort of North American researchers over time. Data for North America are based upon 456 references from Leet & Reilly (1988); those from Japan are based upon 129 references from Ikehara & Kobayashi (1989). Papers were selected on the basis of having *Sebastes, Sebastodes* or rockfish in the title. Papers were assigned to the disciplines by content of the title.

mada 1980), lipid metabolism (Shimma & Tsujigado 1983), temperature tolerance (Ouchi 1977) and ontogeny of immune systems (Nakanishi 1986). Fieldwork on larvae (Kuwahara & Suzuki 1983) and juveniles (Sakai et al. 1985), the latter directed at understanding movements of tagged fish, also has been pursued to better understand ecological requirements of these Japanese species.

The research papers presented in this volume bring together a wide variety of complementary research in the field of reproduction and early life history in *Sebastes*, allowing us to broaden the scope and implications of our studies while identifying future opportunities for collaborative work. Research approaches and, often, goals may differ between the two countries, as noted above. The strengths of each, however, are mutually beneficial. With the cooperative approach fostered by this publication, we hope to bring together these two bases of knowledge and provide significant interchange and continued communication.

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References cited

Ahlstrom, E.H. 1961. Distribution and relative abundance of rockfish (*Sebastodes* spp.) larvae off California and Baja California. Rapp. P.-V. Cons. Perm. Explor. Mer 150: 169–176.

Barsukov, V.V. 1981. A brief review of the sub-family Sebastinae. J. Ichthyol. 21: 1–26.

Barsukov, V.V. & Lo-chai Chen. 1978. Review of the subgenus *Sebastiscus* (*Sebastes*, Scorpaenidae) with a description of a new species. J. Ichthyol. 18: 179–193.

Boehlert, G.W., M. Kusakari, M. Shimizu & J. Yamada. 1986. Energetics during embryonic development in the kurosoi, *Sebastes schlegeli* Hilgendorf. J. Exp. Mar. Biol. Ecol. 101: 239–256.

Boehlert, G.W. & M.M. Yoklavich. 1983. Effects of temperature, ration, and fish size on growth of juvenile black rockfish, *Sebastes melanops*. Env. Biol. Fish. 8: 17–28.

Boehlert, G.W. & M.M. Yoklavich. 1984. Reproduction, embryonic energetics, and the maternal-fetal relationship in the viviparous genus *Sebastes* (Pisces: Scorpaenidae). Biol. Bull. (Woods Hole) 167: 354–370.

Bracken, B. 1987. The history of the rockfish fisheries in Alaskan waters. pp. 51–59. *In:* Proceedings of the International Rockfish Symposium, Anchorage, Alaska Sea Grant Rep. 87–2.

FAO. 1977. Yearbook of fishery statistics. 1976 catches and landings. Fisheries Statistics Series, Food and Agriculture Organization, United Nations, Rome. Vol. 42.

FAO. 1988. Yearbook of fishery statistics. 1986 catches and landings. Fisheries Statistics Series, Food and Agriculture Organization, United Nations, Rome. Vol. 62.

Fujita, S. 1957. On the larval stages of a scorpaenid fish, *Sebastes pachycephalus nigricans* (Schmidt). Jap. J. Ichthyol. 6: 91–93. (in Japanese).

Garrod, D.J. & J.W. Horwood. 1984. Reproductive strategies and the response to exploitation. pp. 367–384. *In:* G.W. Potts & R.J. Wootton (ed.) Fish Reproduction: Strategies and Tactics, Academic Press, London.

Gunderson, D.R. 1984. The great widow rockfish hunt of 1980–1982. N. Amer. J. Fish. Manage. 4: 465–468.

Gunderson, D.R. & T.M. Sample. 1980. Distribution and abundance of rockfish off Washington, Oregon, and California during 1977. Mar. Fish. Rev. 42: 2–16.

Harada, E. 1962. A contribution to the biology of the black rockfish, *Sebastes inermis* Cuvier et Valenciennes. Publ. Seto Mar. Biol. Lab. 10: 307–361.

Hatanaka, M. & K. Iizuka. 1962. Studies on the fish community in the Zostera area. III. Efficiency of production of *Sebastes inermis*. Bull. Jap. Soc. Sci. Fish. 28: 305–313. (in Japanese).

Hoelzer, G. 1987. The effect of early experience on aggression in two territorial scorpaenid fishes. Env. Biol. Fish. 19: 183–194.

Hoshiai, G. 1977. Larvae and juveniles of the scorpaenid fish, *Sebastes schlegeli*. Jap. J. Ichthyol. 24: 35–42. (in Japanese).

Igarashi, T. 1968. Ecological studies on a marine ovoviviparous teleost, *Sebastes taczanowskii* (Steindachner). I. Seasonal changes of the testis. Bull. Fac. Fish. Hokkaido Univ. 19: 19–26. (in Japanese).

Ikehara, K. & T. Kobayashi. 1989. Bibliography of fishes of genus *Sebastes* and subgenus *Sebastiscus*. Jap. Sea Reg. Fish. Res. Lab., Niigata. 55 pp. (in Japanese).

Ikehara, K., M. Nagahara, Y. Yamada & K. Naiki. 1980. Fundamental studies for establishing rockfish culture techniques. V. Feeding experiments on young rockfish, *Sebastes thompsoni* and *S. schlegeli*, during summer season. Bull. Jap. Sea Reg. Fish. Res. Lab. 31: 57–63. (in Japanese).

Ito, D.H., D.K. Kimura & M.E. Wilkins. 1987. Status and future prospects for the Pacific ocean perch resource in waters off Washington and Oregon as assessed in 1986. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-113. 50 pp.

Kusakari, M., Y. Mori & K. Kudo. 1977. Studies on the breeding habit of a rockfish, *Sebastes schlegeli* (Hilgendorf). 2. On the breeding behavior of pregnant fish and the just spawned larvae. J. Hokkaido Fish. Exp. St. 34: 1–11. (in Japanese).

Kuwahara, A. & S. Suzuki. 1983. Vertical distribution and feeding of three species of rockfish Scorpaenidae larvae. Bull. Jap. Soc. Sci. Fish. 49: 515–520. (in Japanese).

Larson, R.J. 1980. Influence of territoriality on adult density in two rockfishes of the genus *Sebastes*. Mar. Biol. 58: 123–132.

Leet, M.H. & C.A. Reilly. 1988. Annotated bibliography of the genus *Sebastes* (family Scorpaenidae). Pacific Marine Fisheries Commission, Portland. 249 pp.

Lenarz, W.H. & T.W. Echeverria. 1986. Comparison of visceral fat and gonadal fat volumes of yellowtail rockfish, *Sebastes flavidus*, during a normal year and a year of El Niño conditions. U.S. Fish. Bull. 84: 743–745.

Mearns, A.J., M.J. Allen, M.D. Moore & M.J. Sherwood. 1980. Distribution, abundance, and recruitment of soft-bottom rockfishes (Scorpaenidae: *Sebastes*) on the southern California mainland shelf. Calif. Coop. Oceanic Fish. Invest. Rep. 21: 180–191.

Mizue, K. 1957. Studies on a scorpaenous fish *Sebastiscus marmoratus* Cuvier et Valenciennes. I. On the monthly variation of gonad maturity. Bull. Fac. Fish. Nagasaki Univ. 5: 27–29. (in Japanese).

Moser, H.G. 1967. Seasonal histological changes in the gonads of *Sebastodes paucispinis* Ayres, an ovoviviparous teleost (family Scorpaenidae). J. Morphol. 123: 329–353.

Moser, H.G. & E.H. Ahlstrom. 1978. Larvae and pelagic juveniles of blackgill rockfish, *Sebastes melanostomus*, taken in midwater trawls off southern California and Baja California. J. Fish. Res. Board Can. 35: 981–996.

Moulton, L.L. 1975. Life history observations on the Puget Sound rockfish, *Sebastes emphaeus* (Starks, 1911). J. Fish. Res. Board Can. 32: 1439–1442.

Nakanishi, T. 1986. Ontogenetic development of the immune response in the marine teleost, *Sebastiscus marmoratus*. Bull. Jap. Soc. Sci. Fish. 52: 473–477.

Norton, J. 1987. Ocean climate influences on groundfish recruitment in the California Current. pp. 73–99. *In:* Proceedings of the International Rockfish Symposium, Anchorage, Alaska Sea Grant Rep. 87–2.

Ohgami, H., N. Katano, T. Sasaki & T. Ohtaki. 1979. Studies on the seedling production of scorpaenous fish, *Sebastiscus marmoratus* Cuvier et Valenciennes. II. The growth during larval stage. Bull. Shizuoka Pref. Fish. Exp. St. 13: 93–100. (in Japanese).

Ouchi, K. 1977. Temperature tolerance of young rockfish, *Sebastes thompsoni* (Jordan et Hubbs). Bull. Jap. Sea Reg. Res. Lab. 28: 1–8. (in Japanese).

Ouchi, K., T. Suzuki & K. Ikehara. 1978. Seasonal histological changes in the testis of *Sebastes thompsoni* (Jordan et Hubbs). Bull. Jap. Sea Reg. Fish. Res. Lab. 29: 121–135. (in Japanese).

Phillips, J.B. 1964. Life history studies on ten species of rockfish (genus *Sebastodes*). Calif. Dep. Fish Game, Fish Bull. 126. 70 pp.

Sakai, K., H. Nagashima & K. Kiso. 1985. Growth and movement of artificially reared young rockfish, *Sebastes schlegeli*, after release in Matsushima Bay. Bull. Tohoku Reg. Fish. Res. Lab. 47: 21–32. (in Japanese).

Sasaki, T. 1976. The larvae of two scorpaenid fishes, *Sebastes wakiyai* and *S. iracundus*. Bull. Jap. Soc. Sci. Fish. 42: 1353–1356.

Shelbourne, J.E. 1964. The artificial propagation of marine fish. Adv. Mar. Biol. 2: 1–83.

Shimizu, M. & J. Yamada. 1980. Ultrastructural aspects of yolk absorption in the vitelline syncytium of the embryonic rockfish, *Sebastes schlegeli*. Jap. J. Ichthyol. 27: 56–63.

Shimma, H. & A. Tsujigado. 1983. Lipids of brood scorpionfish *Sebastiscus marmoratus* and their larvae. Bull. Nat. Res. Inst. Aquacult. 4: 9–19. (in Japanese).

Shiokawa, T & H. Tsukahara. 1961. Studies on habits of coastal fishes in the Amakusa Islands. I. Early life history of the purple rockfish, *Sebastes pachycephalus pachycephalus* Temminck et Schlegel. Rec. Oceanogr. Works Jap. Spec. 5: 123–127.

Takemura, A., K. Takano & K. Yamauchi. 1989. The *in vitro* effects of various steroid hormones and gonadotropin on oocyte maturation of the viviparous rockfish, *Sebastes taczanowskii*. Bull. Fac. Fish. Hokkaido Univ. 40: 1–7.

Trout, G.C. (ed.). 1961. ICES/ICNAF redfish symposium. Int. Comm. Northwest Atl. Fish., Spec. Publ. 3. 311 pp.

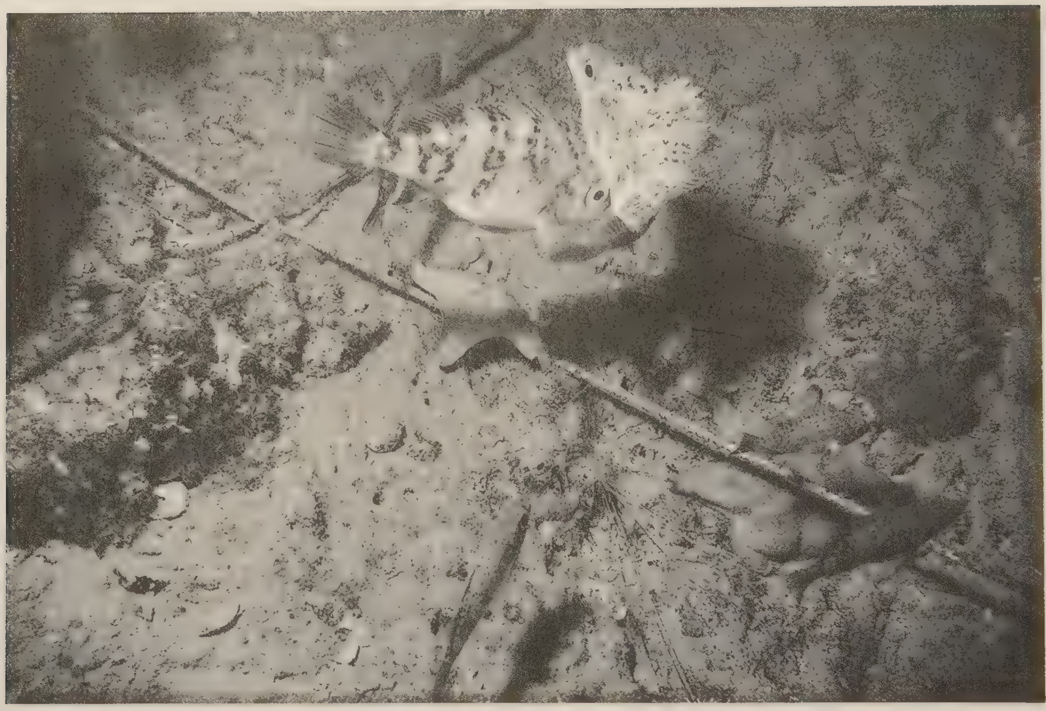
Yamagishi, H., K. Takano & H. Ohta. 1984. Social behaviour of the white-edged rockfish, *Sebastes taczanowskii* (Steindachner). Bull. Fac. Fish. Hokkaido Univ. 35: 1–7. (in Japanese).

Sources to the figures on pp. 30, 90, 134 and 146:

Goode, G.B. & T.H. Bean. 1895. Oceanic ichthyology. U.S. Nat. Mus. (Smithsonian Institution) Special Bull. 2.

Jordan, D.S. & B.W. Evermann. 1896. The fishes of North and Middle America. 4 vol., Bull. U.S. Nat. Mus. 47.

Matsubara, K. 1955. Fish morphology and hierarchy. Ishizaki-shoten, Tokyo. (In Japanese).



Sebastes inermis from Japan: a male (right) and female during courtship; the male's mouth gaped, all of his fins expanded, and posterior half of his body quivered in front of the female; the female's swollen abdomen is noticeable. Photograph by O. Ezaki.

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Bioenergetics and Growth of Northern Anchovy *Engraulis mordax*

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Abstract.–Changes in total body energy content of adult (total length ∼9 cm, wet mass ∼9 g) northern anchovy *Engraulis mordax* were estimated by sampling captive groups swimming at 8.7 and 21.1 cm/s for 12 hours daily. Anchovy were fed euphausiids at rations of 5 and 3.4% of fish wet mass per day (∼54 and 37 cal · g fish wet mass^{-1} · day^{-1}, respectively). Gross energy conversion efficiency increased with ration levels and declined with swimming speed, ranging from 39% to 1%. Dry mass and lipid losses were estimated in fasting fish swimming at the same speeds. Energy losses were 17.6 and 28.2 cal · g fish wet mass^{-1} · day^{-1} at the slow and fast speeds, respectively. The proportion of food energy used for growth and maintenance metabolism was about 65%. A model derived for adult anchovy metabolism was consistent with observed growth and reproduction rates, and the few measurements of ration and swimming speed in nature.

The incorporation of energy from food into growth and reproduction by northern anchovy *Engraulis mordax* has been roughly quantified. Prey abundance influences the rate of anchovy reproduction during subsequent years, according to time-series analysis (Smith and Eppley 1982). Abundant food probably results in more energy intake and storage. Energy available for growth and reproduction by northern anchovy in the wild has been estimated at 12.8% of energy intake, based on laboratory measurements of gross energy-conversion efficiency (Hunter and Leong 1981). At 12.8% efficiency, the daily ration needed for average growth and reproduction was estimated to be 4-5% of fish wet mass (Hunter and Leong 1981), which is towards the high end of the range of field estimates for engraulids (Blaxter and Hunter 1982). However, food intake and energy demands vary. An energy budget model could help explain and predict the effect of food availability on anchovy growth and reproduction.

Gross energy-conversion efficiency is the net energy remaining after food assimilation and metabolic losses divided by the total energy consumed as food. Thus, gross energy-conversion efficiency should tend to increase with ration and decrease with increased swimming activity. The impact of swimming activity on clupeoid metabolism has been described for Pacific sardine *Sardinops caerulea* (Lasker 1970), Atlantic menhaden *Brevoortia tyrannus* (Durbin et al. 1981), and Peruvian anchoveta *E. ringens* (Villavicencio 1981). Estimated metabolic rates of adult northern anchovy (S. Kaupp, R. Lasker, and R. Leong, a table of estimates obtained from J.R. Hunter, Southwest Fish. Sci. Cent., NMFS, NOAA, P.O. Box 271, La Jolla, CA 92037, unpubl. data) are about twice as high as those of its congener, *E. ringens*, at swimming speeds of about 1 body length/s. This difference is not small in relation to the overall energy budget of engraulids; therefore, better estimates of swimming metabolism are needed. The present study measures the energy expended for metabolism by northern anchovy at different swimming speeds, examines the effect of ration and metabolic rate on gross energy-conversion efficiency, and derives a model for adult anchovy metabolism.

Methods

The flume

Juvenile and adult northern anchovy ranging from 2 to 7 g wet mass were purchased from live-bait dealers in February 1984 and acclimated to laboratory conditions for 2–4 months prior to being transferred to an open flume for exercising the fish. Procedures for keeping live anchovy are described in Leong (1971) and Hunter and Leong (1981). Fish were fed 0.09 g Biomet trout pellets per fish per day until the study began.

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Fishery Bulletin, U.S. 89:555–566 (1991).

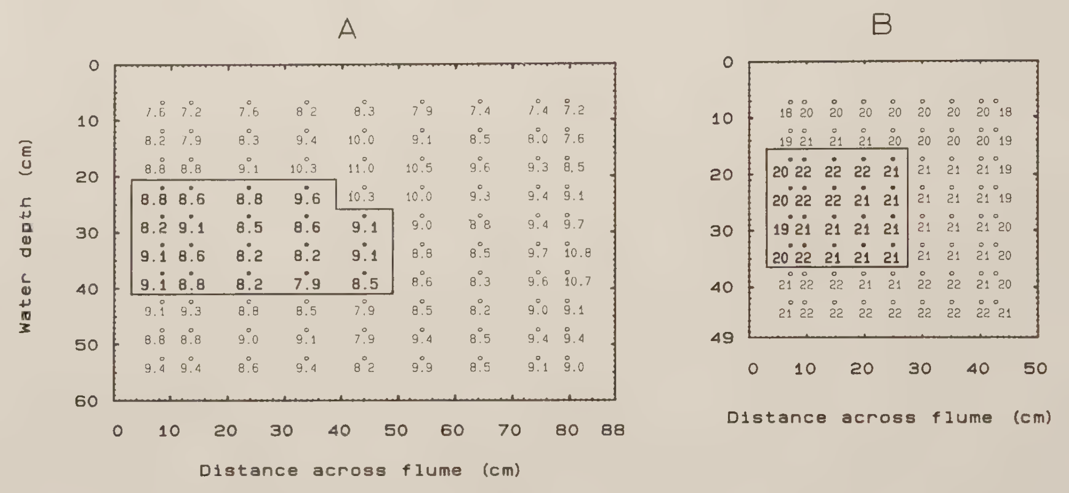

Figure 1

Cross-sections of two flume sections showing water speed (in cm/s). Outlined areas were habitually occupied by the fish, and the enclosed speed values (shown in bold) were averaged to obtain the swimming speed in the (A) slow and (B) fast sections.

The open flume was composed of two connected sections, the second section narrower and shallower than the first, resulting in a more rapid flow. The first section (the slow section) measured 244×88×60 cm (1290 L), and the second (the fast section) measured 244×50×49 cm (600 L). A 20 hp pump at the downstream end of the flume recirculated about 50 L/s of seawater through a feed pipe back to the upstream end of the flume. Water flowed through a tapered expansion section packed with gratings to even the flow. The whole flume was inside a 15,000 L tank. Fresh filtered seawater was added to the recirculating water in the flume at a rate of 20–30 L/minute. Temperature was maintained at 16.5–17.5°C.

Cross-sectional current profiles in each section were measured with a Marinco B-10 ducted impeller current meter. Baffles upstream from each section were adjusted to make the current profiles as uniform as possible, and gratings at the ends of each section confined the fish. Anchovy acclimated to the flume occupied habitual areas within the two sections (Fig. 1). The current measurements in these areas were averaged to estimate swimming speed. The pump was operated 12 hours daily during "daylight"; the photoperiod was 13L:10D with half-hour "dawn" and "dusk" periods.

Fish were anesthetized with quinaldine prior to transfer to the flume. During transfer, the fish were sorted and selected by size. A greater number were put in the larger (slow) flume section to make fish density similar in both sections. Initially 1600 and 1000 fish were put into the slow and fast sections, respectively. The 12-hour swimming regime was built up over 8–10 days and then maintained for 2–3 weeks for each treatment.

Treatments

Three levels of energy intake—high, zero, and low rations (in that order)—were imposed at two swimming speeds, making a total of six treatment combinations (Table 1). At each ration level, slow- and fast-speed treatments were applied concurrently in the two flume sections. The initial stock of fish was enough for the high- and zero-ration treatments. The flume was restocked for the low-ration treatments, but the number of laboratory-acclimated fish available was low (Table 1).

Starting 8–10 days before the treatments began, food type was changed to commercially obtained frozen euphausiids (species not identified). Anchovy were fed thawed euphausiids for 1 hour (high ration) or 0.5 hour (low ration) during the end of the daily swimming period. Food placed in 15 L containers of water above the flume flowed into perforated tubes (2.5 cm diameter, 0.6 cm perforations) stretched across the front of the two sections. Screens were temporarily inserted

Table 1

Summary of feeding levels in sequence of application, 12-hour enforced speeds, average fish mass, and estimated daily rations for the six treatments using the northern anchovy *Engraulis mordax*. N_C = initial number of fish in each flume section at the start of each treatment, N = total number killed for samples (number of samples in parentheses), and D = percentage of fish that died.

Treatments						Fish mass (g)			
Feeding level	Speed (cm/s)	N_C	N	D (%)	Wet mass of food per fish* (g/day)	Wet	Dry	Corrected daily ration** (% wet mass)	Ration energy (cal·g fish wet mass^{-1}·day^{-1})
High	8.7	1392	331 (4)	39	0.443	9.02	2.40	5.06	55.7
	21.1	674	184 (4)	49	0.442	9.83	2.57	4.73	52.0
0	8.7	469	291 (5)	8	0	8.86	2.68	0	0
	21.1	131	86 (3)	27	0	9.32	2.96	0	0
Low	8.7	416	298 (4)	16	0.227	6.82	1.92	3.42	37.6
	21.1	177	111 (2)	37	0.285	8.67	2.66	3.38	37.2

* Average from daily amounts dispensed and equations in Figure 2.
** Corrected for gastric evacuation (cf. Equation 4 in text).

to prevent food in one section from passing to the other. Uneaten food collected on the screens was weighed.

Rations were chosen to match the high ration (4–5%) estimated by Hunter and Leong (1981), and a lower ration (3%) in the middle of the range of field estimates (Blaxter and Hunter 1982). The zero ration was included so that metabolism could be estimated from the loss of body energy.

Preliminary estimates of rations were made from the net mass of food dispensed and the number of fish in each treatment (Table 1). Preliminary ration estimates were calibrated based on the amount of food in stomachs after feeding, corrected for gastric evacuation. To estimate the gastric evacuation rate, 15–24 fish were killed and stomach contents weighed once per hour for 7 hours on the seventh day of the first treatment.

Removing and counting fish

A sample of fish (Table 2)* was collected in one sweep of a large dipnet at the beginning and end of each treatment, and every 4–7 days during five of the six treatments. In the low-ration, fast-speed treatment there were enough fish only for the initial and final samples. At least 20 fish were planned for each sample, but the number of fish netted was sometimes lower, or much higher (Table 2)* because the sample was taken quickly to avoid disturbing the fish.

The standard length of sampled fish, their wet mass, and the wet mass of stomach contents were measured. A subset of about 20 fish from each sample and the combined stomach contents from 9 samples were dried for 6 days at 55°C, cooled in desiccators, and weighed.

A census was kept on the number of fish in each section of the flume based on rapid counts of the fish transferred to the flume, minus removals due to sampling and mortality. Dead fish were collected and measured each day. The initial counts were accurate to within 10% of the total number collected at the end of the treatments. A corrected census, figured from the total counts, was used in the final calculations.

Data analysis

Within each treatment, trends in sample means (i.e., length) or calculated values (i.e., kcal/fish) were expressed as slopes in relation to elapsed time by using linear regression (method of least squares). When only two samples were collected in a treatment, the difference over time was calculated. The significance of slopes, differences between initial and final sample means, and differences between values estimated from regression (i.e., log of dry mass) were evaluated with t-tests.

Apparent growth trends in some treatments were corrected to account for high mortality of fish smaller than the treatment mean. If there was no significant change in length (e.g., in zero-ration treatments), then no correction for mortality was made and length was assumed to be constant. An approximation of the bias in group mean length caused by mortality each day was calculated as the difference between the apparent mean length of the group each day (L_A) and the mean length calculated by including the dead fish collected that day,

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* In the zero-ration treatments, sample size was the same as the number dried (Table 3).

Table 2

Increase in standard length (95% confidence intervals in parentheses) with time during the four feeding treatments and the correction for size-specific mortality. N_C = number of fish in each flume section before the first sample, N = sample size, N_S = stomach content sample size, and NA = not applicable.

Ration ($cal \cdot g^{-1} \cdot day^{-1}$)	Speed (cm/s)	Day	N_C	N	N_S	Mean length (mm)	Apparent growth in length	Mortality bias	Actual growth in length
							(mm/day)		
High	Slow								
55.7	8.7	0	1392	101	0	88.1 (±1.2)			
		7	1160	168	157*	90.1			
		14	773	29	29	95.4			
		21	556	33	33	91.0 (±2.5)	0.202 (±0.569)	0.155	0.047
High	Fast								
52.0	21.1	0	674	99	0	88.9 (±1.1)			
		7	489	33	33	91.8			
		14	327	22	22	95.4			
		21	187	30	30	94.1 (±2.5)	0.277 (±0.324)	0.244	0.033
Low	Slow								
37.6	8.7	0	416	75	24	84.4 (±1.1)			
		7	319	78	24	84.1			
		14	212	70	24	85.5			
		20	126	75	24	86.0 (±1.3)	0.092 (±0.099)	0.023	0.069
Low	Fast								
37.2	21.1	0	177	52	24	93.9 (±1.7)			
		16	59	59	24	92.9 (±1.7)	−0.063	NA	0

*Total of 8 samples (Fig. 3) collected 0–7 hours after feeding (N_S = 23, 21, 19, 16, 24, 15, 15, and 24, respectively).

Daily bias =

$$L_A - \left[\frac{(L_A N_C) + (L_M N_M)}{N_C + N_M}\right] \text{ mm/day}, \qquad (1)$$

where N_C was the number of fish in the treatment group at the end of each day, N_M was the number of dead fish that day, and L_M was the mean standard length of the dead fish that day. The L_A was calculated from a regression of sample mean lengths on elapsed time over the course of the treatment. The slope of this regression (L_A on elapsed time) was the apparent growth (Table 2), which was corrected by the average of the daily biases to estimate the actual increase in fish length.

Fish mass was estimated from corrected length using log–log regressions of dry mass on standard length for each sample. The regression estimate for each sample was calculated by assuming that length increased at the corrected rate for that treatment.

From each sample, a subset of four fish, chosen to best match the estimated length and dry mass of the sample, was analyzed for fat content by using Soxhlet extraction with chloroform-methanol (2:1). Fat content of food removed from stomachs was also measured. Total energy content of fish and food was estimated from published values (Brett and Groves 1979, Hunter and Leong 1981) for heat of combustion. The rate of energy loss or gain in each treatment was calculated as the regression slope of fish energy content in each sample versus elapsed time.

Results

Rations

Anchovy stomach contents from 12 samples (Table 2) were weighed immediately after feeding. The average amount of food in the stomachs was less than (but correlated with) the net amount of food that was dispensed per fish (Fig. 2). The difference was too large to be due to the rate of gastric evacuation. A portion of the food passed through gaps in the bottom of the flume sections and into the surrounding tank. Recirculation of this food was prevented by screens. Regressions of stomach contents on food dispensed (Fig. 2) suggested that a greater proportion of the food dispensed was eaten in the high-ration, fast-speed treatment than in the other treatments. Although the regressions were not significantly different, they were used to estimate stomach contents separately for each speed on days when stomach contents were not sampled. The average of the resulting daily estimates was calculated for each treatment (Table 1).

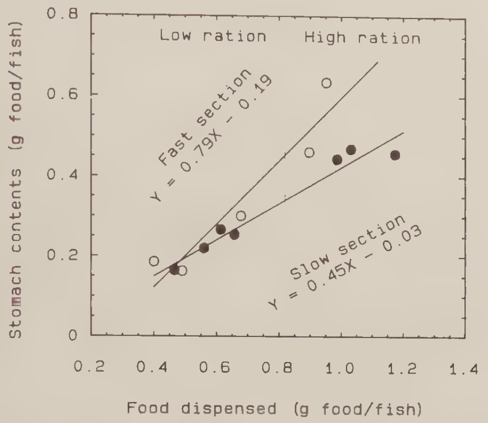

Figure 2

Relationship between the net amount of food dispensed per anchovy and stomach contents (wet mass of food/fish) after feeding in the slow (filled circles) and fast sections (open circles) of the flume. Each point is the mean for a sample of N_S fish (Table 2).

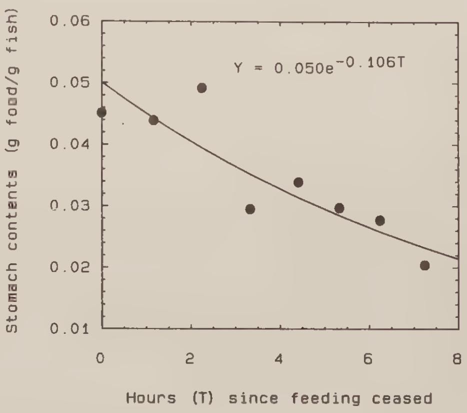

Figure 3

Gastric evacuation rates of northern anchovy fed euphausiids (food wet mass/g wet mass fish). Each point is the mean for a sample of N_S fish (Table 2).

Evacuation of the food from the stomach was slow (Fig. 3). The absence of an immediate decline in stomach contents after feeding suggested a gastric pause or coprophagy, although this result may be due to sampling errors. The following regression (using a semilog transformation) of mean stomach contents (Y in grams food/gram fish) versus elapsed time (T in hours after feeding stopped) describes the data from eight hourly samples (Table 2, Fig. 3):

$$\log_e Y = -2.995 - 0.106\ T \quad (N\ 8,\ r^2\ 0.81). \tag{2}$$

Taking the antilog

$$Y = 0.05\ e^{-0.106\ T}\ \text{g food / g fish}, \tag{3}$$

the actual amount of food consumed (C_T) between the initiation and cessation of feeding was estimated (Elliott and Persson 1978) as

$$C_T = \frac{[S_T - (S_0\ e^{-dT})]\ rT}{1 - e^{-dT}}\ \text{g food}, \tag{4}$$

where S_T was the amount of food found in stomachs at the cessation of feeding, and d = 0.106 (from Equation 3). No food was in the stomachs at the initiation of feeding ($S_0 = 0$). For 1 hour of feeding, C_T equaled 1.054 S_T, and for 0.5 hour of feeding, C_T equaled 1.027 S_T. Thus, only a slight correction of mean stomach content estimates was needed to calculate the rations (Table 1).

The water content of food (euphausiids) averaged 78.4% (*N* 9, SD 1.7%); therefore, dry mass averaged 21.6% of wet mass. The fat content of the food averaged 21.8% of dry mass (*N* 3, SD 3.6). S. Kaupp (NMFS Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92037, pers. commun., March 1984) found that the average protein content of euphausiids (species not identified) was 43.5% of dry mass (*N* 25, SD 0.20). The remaining dry mass (24.7%) was estimated to consist of ash and chitin in roughly equal amounts, since Lasker (1966) found that molts and ash each made up about 10% of dry mass in *Euphausia pacifica*. Assuming 9.2 kcal/g for fat, 5.65 kcal/g for protein, and 4.1 kcal/g for carbohydrate (Brett and Groves 1979), the total caloric content of the food was

$$\left[\frac{21.8}{100}\ 9.2\ \frac{\text{kcal}}{\text{g dry}}\right] + \left[\frac{43.5}{100}\ 5.65\ \frac{\text{kcal}}{\text{g dry}}\right] + \left[\frac{12.4}{100}\ 4.1\ \frac{\text{kcal}}{\text{g dry}}\right] = 5.09\ \frac{\text{kcal}}{\text{g dry food}}$$

and

$$\left[5.09\ \frac{\text{kcal}}{\text{g dry food}}\right]\left[\frac{21.6\text{g dry}}{100\text{g wet food}}\right] = 1.1\ \frac{\text{kcal}}{\text{g wet food}}.$$

Growth in length

Final mean length was significantly higher than the initial mean length in all feeding treatments except the low-ration, fast-speed treatment (t-test, $P \leqslant 0.05$; Table 2). However, the slopes of the regressions describing the apparent rates of growth (in length) were not significantly different from zero, because of the variation not explained by growth or selective mortality. The fish schooling in the flume may have sorted themselves by size so that the dipnet frequently caught a sample containing larger- or smaller-than-average fish. The coefficient of variation of length in each sample ranged from 5 to 7%. The low number of samples would make this an important source of error.

Table 3

Regressions of the natural log of dry mass ($\log_e Y$) on the log of standard length ($\log_e X$) estimated from actual growth (cf. Table 2), and measures of fat content (*N* 4) used to estimate dry mass, total energy, caloric growth, and energy loss during the six treatments. Estimates in brackets assume no increase in length; 95% confidence limits in parentheses. *N* = number of fish dried.

Treatment	Day	*N*	Regression equation	Length (mm)	Log of dry mass from regression	Dry mass (g)	Fat content (%)	Total energy (kcal)
High ration, slow speed								
	0	25	$\log_e Y = 3.861 \log_e X - 16.664$	89.04	0.668 (±0.091)	1.95	36.7	11.70
	7	32	$\log_e Y = 5.241 \log_e X - 22.814$	89.36	0.732	2.08	39.8	12.87
	14	19	$\log_e Y = 4.679 \log_e X - 20.333$	89.69	0.705	2.02	40.9	12.61
	21	23	$\log_e Y = 4.605 \log_e X - 19.784$	90.02	0.939 (±0.059)	2.56	43.9	16.30
				[89.04]	[0.888 (±0.059)]	[2.43]		
High ration, fast speed								
	0	24	$\log_e Y = 5.524 \log_e X - 23.943$	88.68	0.832 (±0.078)	2.30	41.7	14.39
	7	23	$\log_e Y = 3.893 \log_e X - 16.587$	88.91	0.883	2.42	43.7	15.38
	14	12	$\log_e Y = 5.193 \log_e X - 22.467$	89.14	0.851	2.34	43.8	14.89
	21	20	$\log_e Y = 4.574 \log_e X - 19.611$	89.37	0.939 (±0.056)	2.56	44.8	16.42
				[88.68]	[0.903 (±0.060)]	[2.47]		
Low ration, slow speed								
	0	24	$\log_e Y = 4.515 \log_e X - 19.493$	84.06	0.515 (±0.062)	1.67	38.4	10.16
	7	24	$\log_e Y = 4.839 \log_e X - 20.856$	84.54	0.616	1.85	41.1	11.51
	14	24	$\log_e Y = 5.485 \log_e X - 23.712$	85.02	0.657	1.93	39.2	11.83
	20	24	$\log_e Y = 5.539 \log_e X - 24.050$	85.44	0.586 (±0.066)	1.80	40.5	11.15
				[84.06]	[0.496 (±0.067)]	[1.64]		
Low ration, fast speed								
	0	41	$\log_e Y = 3.352 \log_e X - 14.245$	93.4	0.963 (±0.032)	2.62	46.4	17.02
	16	49	$\log_e Y = 3.906 \log_e X - 16.733$	[93.4]	[0.988 (±0.047)]	*[2.62]	46.8	17.07
No food, slow speed								
	0	19	$\log_e Y = 4.587 \log_e X - 19.767$	92.52	1.000 (±0.076)	2.72	46.2	17.38
	4	24	$\log_e Y = 4.975 \log_e X - 21.499$	do.	1.025	2.79	47.6	17.96
	8	23	$\log_e Y = 5.293 \log_e X - 23.041$	do.	0.923	2.52	44.2	15.76
	12	21	$\log_e Y = 4.838 \log_e X - 21.016$	do.	0.888	2.43	45.1	15.36
	16	24	$\log_e Y = 5.611 \log_e X - 24.716$	[92.52]	[0.914 (±0.063)]	[2.49]	43.1	15.56
No food, fast speed								
	0	21	$\log_e Y = 3.553 \log_e X - 14.947$	93.48	1.176 (±0.064)	3.24	45.2	20.97
	6	23	$\log_e Y = 4.903 \log_e X - 21.210$	do.	1.039	2.83	46.8	18.57
	12	42	$\log_e Y = 3.542 \log_e X - 15.066$	[93.48]	[1.007 (±0.051)]	[2.74]	46.1	17.82

* Assumed no change in dry mass since the difference was not significant.

Estimates of actual growth (in length), as corrected for mortality (Table 2), appeared similar to those for 1- to 2-year-old anchovy in nature based on otolith increments (Spratt 1975), but were lower than those measured by Hunter and Leong (1981) in the laboratory. No increase in length was indicated during the low-ration, fast-speed treatment, so no correction was made for mortality. The most rapid length increase (0.069 mm/day) was estimated for the group with the smallest mean size (Table 2). This group underwent the low-ration, slow-speed treatment yet appeared to have a faster rate of growth (in length) than did the high-ration, slow-speed group. This might suggest that the increase in length was size-dependent and somewhat independent of the net energy surplus.

Mortality was highest during the high-ration treatments and lowest in the low-ration and fasting treatments, especially at slow speed (Table 1). Fish bumped into the gratings between flume sections during feeding, which may have led to a high rate of injuries resulting in death. The size bias in mortality might have resulted from large fish being less often injured by the gratings. However, the treatment with the smallest sized fish (low-ration, slow-speed) had one of the lowest mortality rates.

Dry mass

Estimates of fish dry mass for each sample were obtained from mass-on-length regressions (Table 3) by using length estimates corrected for mortality in three feeding treatments (Table 2) and assuming no length change in the other treatments. In all but one case, the final dry mass estimates were significantly greater (high- and low-ration treatments) or lower (zero-ration treatments) than the initial estimates (t-test, $P \leqslant 0.05$). In the zero-ration treatments, the loss of dry mass was more than twice as rapid in the fast-speed treatments as it was in the slow-speed treatments (Table 3). Dry mass increased about four times more rapidly during the high-ration treatments than during the low-ration treatments, and dry mass increased more than twice as rapidly during slow-speed treatments as during fast-speed treatments at both rations. Dry mass did not change significantly between the initial and final estimates when fish were fed the low ration and swam at the fast speed, so growth was assumed to be zero (Table 3).

In three feeding treatments (Table 3) the increases in mass were dependent on estimated increases in length. Although realistic, the corrected length increases (Table 2) may not have been accurate. Therefore, conservative estimates of mass increases in the feeding treatments were calculated by assuming that there was no increase in length (Table 3). A significant length-specific increase over initial dry mass was found in the slow-speed, high-ration treatment.

Caloric growth and gross conversion efficiency

Fat content (Table 3) increased substantially during the high-ration treatments, wherein about 70% of the increase in dry mass was fat. Fat increased about twice as much in the high-ration, slow-speed treatment as in the high-ration, fast-speed treatment. No strong trends in percent fat were found in the low-ration treatments.

The average percent fat of each sample was used to calculate mass of fat and fat-free dry mass per fish. Then the total fish energy content for each sample was calculated (Table 3) by assuming heat of combustion values equal to 29 kcal/g for fat-free dry mass and 9.227 kcal/g for fat (Hunter and Leong 1981).

The trends in total energy content from all of the treatments (Fig. 4) were consistent with a simple energy budget in which more food energy taken in (R), or less energy required for metabolism (Q), results in more energy available for reproduction (S), growth (G), and fat storage (F):

$$R = Q + X + I + S + G + F \text{ cal.} \qquad (5)$$

Components of the energy budget that were not individually estimated were excretion (X) and digestive losses (I). No spawning occurred during the experiments, although gonad mass changed. In the following analyses, changes in gonad and somatic mass were combined as overall growth (B) and fat storage (F). Metabolism was separated into maintenance metabolism (Q_M) and the metabolism associated with extracting usable energy from food (SDA). Ninety percent of the energy losses during starvation were assumed to be respired (Q_M), with excretion accounting for the remainder. This is consistent with estimates of endogenous excretion given by Durbin and Durbin (1981, 1983). The "metabolizable fraction" of fasting energy losses has been assumed to be as little as 80% (Brett 1973) for energy derived from body protein. In the present study, about one-third to one-half of the calories lost during fasting were derived from protein.

Energy losses during fasting were greatest during the fast-speed treatment ($28.2 \text{ cal} \cdot \text{g fish wet mass}^{-1} \cdot \text{day}^{-1}$)** and lowest during the slow-speed treatment ($17.6 \text{ cal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$, Fig. 4). Growth (in $\text{cal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$) was greater at both speeds when rations (R) were high than when they were low (Fig. 4). At both

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** Hereafter the unit of mass (g^{-1}) refers to fish wet mass.

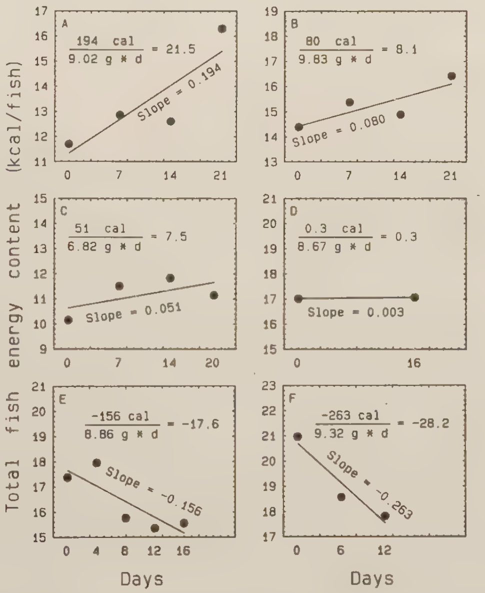

Figure 4

Estimated rates of changes in fish energy content. Slopes were converted into mass-specific rates of caloric growth at the high-ration level for (A) slow-swimming and (B) fast-swimming speeds and at the low-ration level for (C) slow-swimming and (D) fast-swimming speeds. Negative slopes from the zero-ration treatments were converted into mass-specific rates of energy loss for (E) slow-swimming and (F) fast-swimming speeds.

feeding levels, caloric growth was greater in the slow-speed than in the fast-speed treatments. In each treatment, energy utilization (in cal $\cdot$ g^{-1} $\cdot$ day^{-1}) not accounted for by maintenance metabolism (Q_M) and caloric growth (B + F) was a relatively constant fraction of the energy consumed:

	Ration (R)		Growth (B+F)		Maintenance (Q_M)		Excretion (X) + Digestive losses (I) + SDA	
High ration, slow speed:	55.7	−	21.5	−	0.9(17.6)	=	20.1	= 0.36R
High ration, fast speed:	52.0	−	8.1	−	0.9(28.2)	=	18.5	= 0.36R
Low ration, slow speed:	37.6	−	7.5	−	0.9(17.6)	=	14.3	= 0.38R
Low ration, fast speed:	37.2	−	0.3	−	0.9(28.2)	=	11.5	= 0.31R
								Mean 0.35R

About 35% of the food energy was lost through excretion (X), digestive losses (I), and SDA, so the energy budget Equation (5) may be simplified as

$$R = (B + F + Q_M) / 0.65 \text{ cal} \cdot g^{-1} \cdot \text{day}^{-1}. \quad (6)$$

Observed gross conversion efficiency (K) was calculated by dividing caloric growth (B + F) by ration (R). Gross conversion efficiency predicted by the energy budget approximation (Equation 6) was

$$K = \frac{R - (0.35\ R) - Q}{R} \text{ (dimensionless).} \quad (7)$$

The model closely matched the observed gross conversion efficiencies:

	Gross conversion efficiency (%)	
	Observed	Equation (7)
High ration, slow speed:	39	37
High ration, fast speed:	16	16
Low ration, slow speed:	20	23
Low ration, fast speed:	1	−3

These results indicate that a simple energy budget model, assuming a loss of 35% of the food energy due to X, I, and SDA, explains increased growth with increased ration and decreased growth with increased activity.

Discussion

Gross conversion efficiencies

The energy budget approximation (Equation 7) implies that gross conversion efficiency is reduced by low ration and high activity. This was supported by the lower

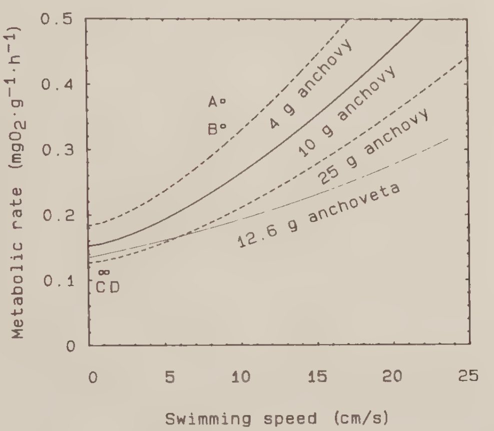

Figure 5

Comparison of other engraulid metabolic rate estimates with model predictions for 4, 10, and 25 g northern anchovy at 17°C. The anchoveta curve is from Villavicencio (1981, temp. 17°C). Respiration rates of (A) actively swimming 10 g northern anchovy at 15°C and, based on energy losses during zero-ration treatments, (B) exercised 16.9–17.8 g fish at 21°C, (C) non-exercised 13.5–16.9 g fish at 18°C, and (D) non-exercised 12.3 g fish at 15.2°C as measured by Kaupp et al. (unpubl. data).

K values in treatment combinations with low ration or high speed compared with the high-ration, slow-speed treatment. Contrarily, K values in the high-ration, slow-speed treatment were much higher than the 12.8% reported by Hunter and Leong (1981) for northern anchovy even though the fish in the present study were exercised and fed smaller rations. Hunter and Leong (1981) fed fish 124 cal · g^{-1} · day^{-1} of semi-dry, pelleted trout food (the caloric equivalent of a ration of 16% of wet body mass/day in copepods). At very high rations, the proportion of food energy lost to X, I, and SDA may increase (Paloheimo and Dickie 1966, Brett 1979, Brett and Groves 1979), causing K to decline.

The euphausiids used for food and the rations (Table 1) in the present study were similar to the zooplankton rations of 1.4–4.9% observed in nature (Blaxter and Hunter 1982). So, although X, I, and SDA vary with food composition (Elliott 1976b, Brett and Groves 1979, Tandler and Beamish 1979 and 1980) and may increase at ration levels higher than those in nature, the energy budget generalizations in Equations (6) and (7) should be applicable to adult anchovy in the wild.

The observed range of gross conversion efficiencies (1–39%) extended higher than the range reported for clupeoids (7–13.5%, Takahashi and Hatanaka 1960, De Silva and Balbontin 1974, Hunter and Leong 1981, Blaxter and Hunter 1982). However, gross conversion efficiencies this high are found in many juvenile fishes (60% Hatanaka and Takahashi 1956, 34% Elliott 1976a, 10–25% Brett and Groves 1979). The importance of different results in such studies is difficult to judge, because of differences in the assumptions, expressions (percentages of mass or energy), experimental conditions (size, maturity, temperature, activity), and the rarity of error estimates.

A model for adult anchovy metabolism

A model for anchovy metabolism was derived by using the estimates from the present study, data on closely related species, and general principles relating swimming speed and metabolism to fish size. The model required estimates of (1) standard metabolism, (2) swimming metabolism, (3) the effect of fish size on standard and swimming metabolism, and (4) the effect of temperature. These estimates are provided in the following sections.

Standard metabolism Standard metabolism was estimated by extrapolating to zero swimming speed from the rates estimated at two speeds. An exponential relationship (Brett 1964) was assumed,

$$Q_M = ae^{bV} \text{ cal} \cdot g^{-1} \cdot \text{day}^{-1}, \qquad (8)$$

where the metabolic rate exclusive of SDA (Q_M) consists of standard metabolism ($Q_0 = a$) increased by a factor (e^{bV}) for the cost of swimming, where V is swimming speed. The energy losses measured in the present study resulted from fish exercising half the time and resting half the time, so

$$Q_M = [0.5\,(ae^{bV})] + [0.5\,(a)] \text{ cal} \cdot g^{-1} \cdot \text{day}^{-1}. \qquad (9)$$

The metabolic rate estimates ($Q_M = 0.9 \times 17.6 = 15.8$, and $0.9 \times 28.2 = 25.4$ cal · g^{-1} · day^{-1}) from the two exercise levels (V = 8.7 and 21.1 cm/s, respectively) were substituted for Q_M and V in Equation (9). The resulting simultaneous equations were solved, and Q_0 was calculated to be 12.1 cal · g^{-1} · day^{-1} at V = 0. Assuming an oxycalorific equivalent of 3.24 cal/mg O_2 (Elliott and Davison 1975), the standard metabolic rate was 0.156 mg $O_2 \cdot g^{-1} \cdot h^{-1}$. Assuming the same metabolizable fraction (0.9) and oxycalorific equivalent, energy losses of 9.7 cal · g^{-1} · day^{-1} at the lowest activity levels measured by S. Kaupp et al. (unpubl. data,) amounted to 0.112 mg $O_2 \cdot g^{-1} \cdot h^{-1}$. The standard metabolism of 12.6 g anchoveta at 17°C (Villavicencio 1981) was 0.135 mg $O_2 \cdot g^{-1} \cdot h^{-1}$. These values (Fig. 5) were similar to the estimate of Q_M in the present study.

Swimming metabolism Standard metabolism ($Q_0 =$ 12.1 $\mathrm{cal \cdot g^{-1} \cdot day^{-1}}$) subtracted from the Q_M estimates for fish at the two speeds left 3.7 and 13.3 $\mathrm{cal \cdot g^{-1} \cdot day^{-1}}$, respectively, for the metabolic cost of swimming (Q_V) for 12 hours a day at 8.7 and 21.1 cm/s. On an hourly basis, Q_V amounted to 0.308 and 1.11 $\mathrm{cal \cdot g^{-1} \cdot h^{-1}}$, respectively. A linear fit to log-transformed estimates of Q_V versus log-transformed V indicated that

$$Q_V = (0.0137\ V^{1.44})\ \mathrm{cal \cdot g^{-1} \cdot h^{-1}}. \qquad (10)$$

For extrapolating beyond the range of measurements, a power function makes a good model for swimming metabolism, because mechanical principles and empirical evidence (Ware 1978, Wu and Yates 1978) indicate that thrust and drag in swimming fish are power functions of speed.

Effect of fish size Fish size was not manipulated in the present study, so size effects could not be quantified from the results. However, reviews (Winberg 1956, Brett and Groves 1979) of results from a large number of studies have led to the generalization that the mass exponent of standard metabolism in fishes is close to 0.8. The corresponding mass-specific exponent (−0.2) combined with the estimate of Q_0 from the present study results in this model,

$$\begin{aligned} Q_0 &= 18.8\ M^{-0.2}\ \mathrm{cal \cdot g^{-1} \cdot day^{-1}} \\ &= 0.783\ M^{-0.2}\ \mathrm{cal \cdot g^{-1} \cdot h^{-1}}, \qquad (11) \end{aligned}$$

where M is anchovy wet mass (∼9g in the present study).

The effect of fish size on the cost of swimming can be modeled by expressing speed relative to length so that the cost of swimming at the normalized speed is the same for any size of fish. The cost of swimming in sockeye salmon *Oncorhynchus nerka*, obtained by subtracting standard metabolism from total metabolism of 8–54cm salmon swimming at speeds of 13–143 cm/s (Brett 1965), can be accurately described by a power function of the Reynolds number (Wu and Yates 1978). The Reynolds number combines fish length, speed, and kinematic viscosity. A similar way of expressing this relationship, which matches Brett's (1965) results (at 15°C) extremely closely, is

$$Q_V = 8.7934 \left[\frac{V}{L^{0.64}} \right]^{1.71} \mathrm{mg\ O_2 \cdot kg^{-1} \cdot h^{-1}}. \qquad (12)$$

Thus, for different sizes of sockeye salmon, the cost of swimming is the same when speed (V) divided by fish length (L in cm) to the 0.64 power is the same. This relationship is also reflected in length exponents (0.5–0.7) for endurance speed in fishes (Bainbridge 1962, Hunter 1971). Note that dividing V by L (body lengths/second) does not normalize speed with respect to swimming cost or endurance. For anchovy, the present study assumed that the length exponent for normalized speed was 0.6. Then, from Equation (10)

$$Q_V = 0.095 \left[\frac{V}{L^{0.6}} \right]^{1.44} \mathrm{cal \cdot g^{-1} \cdot h^{-1}}, \qquad (13)$$

and the cost of swimming in anchovy can be estimated for any size and swimming speed.

Effect of temperature Anchovy metabolic rates were estimated at only one temperature (17°C) in the present study, but the effect of temperature on engraulid anchovy metabolism was estimated for Peruvian anchoveta (Villavicencio 1981) at 14–20°C. These data indicated an increase of 78% in total respiration rate over a change of 6°C. Applying this intensity of temperature effect to the model would amount to

$$Q' = 2.046\ Q\ e^{0.0959\ T}\ \text{(in any units)}, \qquad (14)$$

where Q is the metabolic rate (in any units) at 17°C, and T is the ambient temperature (°C). However, short-term temperature acclimation periods in the laboratory (Villavicencio 1981) may result in greater metabolic rate changes than in the long term in nature. Estimates from Equation (14) should be viewed skeptically, until better estimates of the effect of temperature on anchovy metabolism can be found.

Evaluation of the model

Estimates of maintenance metabolism ($Q_M = Q_0 + Q_V$) from the model (Equations 11 and 13) for 4, 10, and 25g northern anchovy at 17°C were compared with other data on engraulids (Fig. 5), assuming an oxycalorific equivalent of 3.24 cal/mg O_2 (Elliott and Davison 1975). Oxygen consumption of northern anchovy swimming at about 9cm/s in an annular respirometer was 0.38mg $\mathrm{O_2 \cdot g^{-1} \cdot h^{-1}}$ (Kaupp et al. unpubl. data). The rate of energy loss in fasting northern anchovy swimming in a flume at about 9cm/s was 29.3 $\mathrm{cal \cdot g^{-1} \cdot day^{-1}}$ or 0.34mg $\mathrm{O_2 \cdot g^{-1} \cdot h^{-1}}$ (Kaupp et al. unpubl. data, energy loss multiplied by 0.9, the metabolizable fraction). These data were about twice as high as the tunnel respirometry data on anchoveta (Villavicencio 1981) swimming at 9cm/s (Fig. 5). The model predicts metabolic rates in the middle of this range, indicating that it may provide reasonable estimates for engraulid metabolism.

To use the model to estimate ration, the energy required for standard metabolism (Equation 11) and the cost of swimming (Equation 13 converted to $\text{cal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$) plus the energy needed for growth or reproduction, are multiplied by 1/0.65 (from Equation 6) to account for X, I, and SDA. The result is the daily food energy requirement. Similarly, 65% of food energy minus standard and swimming metabolism gives the surplus available for growth and reproduction at that level of food intake and activity.

Hunter and Leong (1981) estimated the food energy requirements of 1-year-old anchovy (wet mass 10.3 g, length 10.3 cm) at 33.8 $\text{cal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ (copepods at 4% of wet mass/day). According to the model in the present study, X, I, and SDA remove 11.8 $\text{cal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$, and standard metabolism (Equation 11) is 11.8 $\text{cal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$. Supposing 1-year-old anchovy swim at 12 cm/s for 12 hours each day, this costs 0.45 $\text{cal} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ (Equation 13), or 5.4 cal/g. If they swim at 2 cm/s for the other 12 hours, this costs another 0.4 cal/g, making the total swimming cost 5.8 $\text{cal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$. Subtracting all these costs from the ration energy leaves 4.4 $\text{cal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$, which Hunter and Leong (1981) estimated to be enough for normal growth plus 20 spawnings per year.

Is this level of swimming activity realistic? Using sonar tracking and Doppler shift analysis, Holliday (1977) measured a relatively uniform swimming speed averaging 45 cm/s over a 40-minute interval for what were thought to be northern anchovy about 14 cm long (25 g). To swim for 12 hours a day at this speed, while maintaining normal growth and spawning 20 times per year, 3-year-old anchovy (Hunter and Leong 1981) would require a ration of 7.7% of body weight per day. However, 3 hours a day at this speed, with the rest of the day at 3 cm/s, would allow for the same growth and reproduction on a ration of only 4%.

It appears that anchovy growth rates in nature and the estimate of spawning 20 times per year (Hunter and Leong 1981) are consistent with the current study's model predictions for anchovy swimming at speeds and consuming rations similar to those observed in nature. Three aspects of the model were determined by experiment: (1) A constant proportion of food energy is available for metabolism and growth, (2) metabolism increases with swimming speed, and (3) gross energy conversion efficiency is a function of ration level and activity. The model should be useful in estimating the effect of changing food abundance on spawning frequency and growth, particularly as more measurements of activity become available.

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Citations

Bainbridge, R.
1962 Training, speed and stamina in trout. J. Exp. Biol. 39: 537–555.
Blaxter, J.H.S., and J.R. Hunter
1982 The biology of the clupeoid fishes. *In* Blaxter, J.H.S., F.S. Russell, and R. Yonge (eds.), Advances in marine biology, vol. 20, p. 1–223. Academic Press, London.
Brett, J.R.
1964 The respiratory metabolism and swimming performance of young sockeye salmon. J. Fish. Res. Board Can. 21: 1183–1226.
1965 The relation of size to rate of oxygen consumption and sustained swimming speed of sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can. 22:1491–1501.
1973 Energy expenditure of sockeye salmon, *Oncorhynchus nerka*, during sustained performance. J. Fish. Res. Board Can. 30:1799–1809.
1979 Environmental factors and growth. *In* Hoar, W.S., D.J. Randall, and J.R. Brett (eds.), Fish physiology, vol. 8, p. 599–675. Academic Press, NY.
Brett, J.R., and T.D.D. Groves
1979 Physiological energetics. *In* Hoar, W.S., D.J. Randall, and J.R. Brett (eds.), Fish physiology, vol. 8, p. 279–352. Academic Press, NY.
De Silva, S.S., and F. Balbontin
1974 Laboratory studies of food intake, growth and food conversion of young herring, *Clupea harengus* (L.). J. Fish Biol. 6:645–658.
Durbin, E.G., and A.G. Durbin
1981 Assimilation efficiency and nitrogen excretion of a filter-feeding planktivore the Atlantic menhaden, *Brevoortia tyrannus* (Pisces: Clupeidae). Fish. Bull., U.S. 79:601–616.
1983 Energy and nitrogen budgets for the Atlantic menhaden, *Brevoortia tyrannus* (Pisces: Clupeidae), a filter-feeding planktivore. Fish. Bull., U.S. 81:177–199.
Durbin, A.G., E.G. Durbin, P.G. Verity, and T.J. Smayda
1981 Voluntary swimming speeds and respiration rates of a filter-feeding planktivore, the Atlantic menhaden, *Brevoortia tyrannus* (Pisces: Clupeidae). Fish. Bull., U.S. 78:877–886.
Elliott, J.M.
1976a The energetics of feeding, metabolism, and growth of brown trout (*Salmo trutta* L.) in relation to body weight, water temperature and ration size. J. Anim. Ecol. 45:923–948.
1976b Energy losses in the waste products of brown trout (*Salmo trutta* L.). J. Anim. Ecol. 45:561–580.
Elliott, J.M., and W. Davison
1975 Energy equivalents of oxygen consumption in animal energetics. Oecologia (Berl.) 19:195–201.

Elliott, J.M., and L. Persson

1978 The estimation of daily rates of food consumption for fish. J. Anim. Ecol. 47:977–991.

Hatanaka, M., and M. Takahashi

1956 Utilization of food by mackerel, *Pneumatophorus japonicus* (Houttuyn). Tohoku J. Agric. Res. 7:51–57.

Holliday, D.V.

1977 Two applications of the Doppler effect in the study of fish schools. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 170: 21–30.

Hunter, J.R.

1971 Sustained speed of jack mackerel, *Trachurus symmetricus*. Fish. Bull., U.S. 69:267–271.

Hunter, J.R., and R. Leong

1981 The spawning energetics of female northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 79:215–230.

Lasker, R.

1966 Feeding, growth, respiration, and carbon utilization of a euphausiid crustacean. J. Fish. Res. Board Can. 23: 1291–1317.

1970 Utilization of zooplankton energy by a Pacific sardine population in the California Current. *In* Steele, J. H. (ed.), Marine food chains, p. 265–284. Oliver and Boyd, Edinburgh.

Leong, R.

1971 Induced spawning of the northern anchovy, *Engraulis mordax* Girard. Fish. Bull., U.S. 69:357–360.

Paloheimo, J.E., and L.M. Dickie

1966 Food and growth of fishes. III. Relations among food, body size, and growth efficiency. J. Fish. Res. Board Can. 23:1209–1248.

Smith, P.E., and R.W. Eppley

1982 Primary production and the anchovy population in the Southern California Bight: Comparison of time series. Limnol. Oceanogr. 27:1–17.

Spratt, J.D.

1975 Growth rate of the northern anchovy, *Engraulis mordax*, in southern California waters, calculated from otoliths. Calif. Fish Game 61:116–126.

Takahashi, M., and M.A. Hatanaka

1960 Experimental study on utilization of food by young anchovy, *Engraulis japonicus* Temminck et Schlegel. Tohoku J. Agric. Res. 11:161–170.

Tandler, A., and F.W.H. Beamish

1979 Mechanical and biochemical components of apparent specific dynamic action in largemouth bass, *Micropterus salmoides* Lacépède. J. Fish Biol. 14:343–350.

1980 Specific dynamic action and diet in largemouth bass, *Micropterus salmoides* (Lacépède). J. Nutr. 110:750–764.

Villavicencio, Z.

1981 Investigacion preliminar de los requerimientos energeticos de anchoveta adulta (metabolismo estandar y actividad). Bol. Inst. Mar Peru (Callao) Vol. extraord., p. 193–205 (ISSN Q378-7699) [in Spanish].

Ware, D.M.

1978 Bioenergetics of pelagic fish: Theoretical change in swimming speed and ration with body size. J. Fish. Res. Board Can. 35:220–228.

Winberg, G.G.

1956 Intensivnost obmena i pishchevye potrebnosti ryb. (Rate of metabolism and food requirements of fishes.) Nauchn. Tr. Belorussk. Gos. Univ. Minsk, 253 p. (Transl. Ser. 194, Fish. Res. Board Can., 1960).

Wu, T.Y., and G.T. Yates

1978 III. A comparative mechanophysiological study of fish locomotion with implications for tuna-like swimming mode. *In* Sharp, G.D., and A.E. Dizon (eds.), The physiological ecology of tunas, p. 313–337. Academic Press, NY.

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Responses of Swimming Skipjack (*Katsuwonus pelamis*) and Yellowfin (*Thunnus albacares*) Tunas to Acute Hypoxia, and a Model of Their Cardiorespiratory Function

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Abstract

Heart rate and swimming-speed responses to acute hypoxia were measured in skipjack (Katsuwonus pelamis) *and yellowfin tunas* (Thunnus albacares). *Swimming speeds began to increase in both species when* O_2 *tension* (Po_2) *reached approximately 124 mmHg. Bradycardia became significant in both species when* Po_2 *reached approximately 130 mmHg. Heart rate fell with* Po_2 *in yellowfin tuna, but, in skipjack tuna, it increased at the lowest* O_2 *levels reached (89–70 mmHg). Bradycardia occurred in both species despite concomitant increases in swimming speed. A continuous infusion dye dilution system was used to monitor changes in ventilation volume* ($\dot{V}_g$) *during hypoxia in yellowfin tuna. As* Po_2 *fell,* $\dot{V}_g$ *increased. At the lowest* O_2 *levels (109–90 mmHg),* $\dot{V}_g$ *was 45% higher than during normoxia. Ventilation volume increased despite no concomitant increases in swimming speed. Data from these experiments were used to develop a model capable of predicting* O_2 *demand and delivery, maximum sustainable (i.e., aerobic) swimming speeds, and minimum survivable* O_2 *levels for yellowfin and skipjack tunas. Results from the model indicate that the cardiorespiratory system of tunas is capable of maximum rates of* O_2 *delivery, even at low swimming speeds, that are approximately three times those of other active teleosts. We believe that, because the pelagic environment provides no place to hide and rest following exhaustive activity, the ability of the cardiorespiratory system of tunas to deliver* O_2 *to the tissues at high rates evolved for the rapid repayment of* O_2 *debts rather than to permit exceptionally high sustained swimming speeds.*

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Introduction

Because of their daily vertical migrations, tunas often encounter reduced ambient O_2, and ambient O_2 levels appear to strongly influence their movements, depth distributions, and vulnerability to specific fishing-gear types (Ingham, Cook, and Hausknecth 1977; Barkley, Neill, and Gooding 1978; Sharp 1978; Sund, Blackburn, and Williams 1981; Hanamoto 1987). Dizon (1977) was apparently the first to directly observe the responses of tunas to lowered ambient O_2. He found that skipjack tuna (*Katsuwonus pelamis*) exposed to hypoxia (Po_2 70–85 mmHg) increased swimming speed, whereas yellowfin tuna (*Thunnus albacares*) did not. He hypothesized that only the former were stressed at this level of hypoxia. Understanding this apparent interspecific difference was the impetus for experiments by Bushnell, Brill, and Bourke (1990) on the cardiorespiratory responses to acute hypoxia of spinally blocked (i.e., paralyzed) skipjack and yellowfin tunas. They found that both species responded to even mild hypoxia (115 mmHg) by increasing mouth gape and ventilation volume ($\dot{V}_g$) and decreasing heart rate (HR).

Using spinally blocked animals affords the opportunity to measure a number of physiological variables simultaneously; however, it eliminates a potentially important response to hypoxia of obligate ram-ventilating fishes like tunas, namely, an increase in swimming speed. By measuring HR, $\dot{V}_g$, and swimming speed of skipjack and yellowfin tunas during normoxia and hypoxia, this study sought to determine what influences the inability to swim has on the physiology of these tunas in normoxia and on their responses to hypoxia.

Because swimming tunas cannot tow multiple cannulas for extended periods (Jones, Brill, and Mense 1986; Jones et al. 1990), we undertook two separate experiments. The first evaluated changes in HR and swimming speed, and the second, changes in $\dot{V}_g$ and swimming speed in response to acute hypoxia. In the latter experiment, the O_2 tensions of exhalant water samples (Peo_2) were analyzed to determine utilization (U, i.e., percent of O_2 in the inhalant water extracted by the gills) and O_2 consumption ($\dot{V}o_2$). This is only the second time these parameters have been measured simultaneously in swimming tunas in normoxia (the first was by Jones et al. 1990) and the first time they have ever been measured in hypoxia. These data are relevant to evaluating the performance of the cardiorespiratory systems of tunas specifically and of obligate ram-ventilating fishes in general.

We also used our data to reanalyze Dizon's (1977) model that evaluated the effects of increasing swimming speed or increasing mouth gape on O_2

delivery during normoxia and hypoxia in skipjack tuna. His model was based on the assumptions that O_2 demand increases exponentially with speed, whereas, without an increase in gape, O_2 delivery increases linearly. Dizon (1977) concluded that increases in swimming speed, without concomitant increases in gape, would result in O_2 demand exceeding O_2 delivery during hypoxia. We undertook a reanalysis because many of the parameters Dizon (1977) used had not been measured or were based on data that have since been shown to be incorrect. In addition, we extended his model to include yellowfin tuna.

Material and Methods

Yellowfin and skipjack tunas were purchased from local commercial fishermen and maintained in outdoor tanks at the National Marine Fisheries Service's Kewalo Research Facility in Honolulu, Hawaii. Water temperature in the tanks was 25° ± 2°C. Animal procurement, handling, and maintenance procedures are further described in Nakamura (1972); Queenth and Brill (1983); and Chang, Brill, and Yoshida (1983). Food was provided daily but was withheld for 24 h prior to an experiment to allow sufficient time for gut clearance (Magnuson 1969).

Experiments were conducted in an indoor 5,300-L doughnut-shaped tank (outside diam, 6.1 m; inside diam, 4.4 m); the inner portion of the tank was dry. Water height was set by an external standpipe and maintained at 37 cm. Seawater (25°C) was introduced to the tank through two sets of concentric polyvinyl chloride (PVC) pipes on the bottom of the swimming channel. Evenly spaced holes in the pipes delivered water to all portions of the tank simultaneously and kept the water well mixed.

The Po_2 of the water supplying the test tank was switched among three sources: normoxic water ($\approx$150 mmHg), hypoxic water (20–30 mmHg), and hyperoxic water (275–300 mmHg). The hyperoxic water was used to bring the tank water back to full O_2 saturation after a hypoxic trial. The Po_2 of the water in the test tank (Pio_2) was continuously monitored with a Radiometer polarographic electrode, mounted in a flow-through cuvette and connected to a Radiometer PHM 71 blood-gas analyzer. Electrode temperature was controlled by pumping water from the test tank through a surrounding water jacket. The Pio_2 was recorded every minute, either by hand or by connecting the blood-gas analyzer's analog output to a Hewlett-Packard (HP) 3455A digital voltmeter. In the latter case, the analog signal was digitally converted to Po_2 by the voltmeter and recorded by an HP 5150A thermal printer. A Yellow Springs Instrument portable O_2 meter was occasionally used to sample Po_2 around the tank to ensure that the tank water remained well mixed throughout an experiment.

Swimming speeds were measured by recording the time to complete one full lap around the tank (generally about 45 s). Swimming patterns were differentiated as laps swum close to the inside wall, in the middle of the channel, or near the outside wall; the corresponding circumferences were used to calculate swimming speed in centimeters per second ($cm \cdot s^{-1}$) and body lengths per second ($BL \cdot s^{-1}$).

Heart Rate Experiment

Heart rates were monitored with electrocardiogram (ECG) electrodes (silver-plated copper wires) inserted subcutaneously over the heart. Electrodes were held in place near their points of insertion and at the posterior margin of the first dorsal fin with sutures (yellowfin tuna) or tiny (no. 85 Eagle Claw) stainless steel hooks (skipjack tuna). Seven skipjack tuna (fork length, 41.8–48.5 cm; body weight, 1.062–2.240 kg) and six yellowfin tuna (fork length, 33.8–57.2 cm; body weight, 0.630–3.390 kg) were used.

For yellowfin tuna, ECG electrodes were implanted under general anesthesia. The anesthetic used was $NaHCO_3$-buffered tricaine methanesulfonate (MS-222). The animals were revived in the test tank by pumping fresh seawater over their gills. Complete anesthesia and revival procedures are described in Jones et al. (1986, 1990). Total elapsed time, from initial anesthesia to full recovery of swimming ability, was approximately 25 min. Fish were given an additional hour to recover before the first hypoxic trial.

For unknown reasons, skipjack tuna often do not survive for long when forced to swim following recovery from anesthesia. Skipjack tuna were therefore handled differently. To minimize stress, fish were moved to the test tank the night before they were to be used in an experiment. On the following day, they were dip netted and gently restrained, ventral side up, on a padded table while seawater was pumped over their gills. Electrocardiogram wires were inserted subcutaneously, and the fish were immediately returned to the test tank. The entire procedure generally took less than 3 min. The fish were allowed 1 h to recover before the first hypoxic trial.

The ECG signal was recorded either by connecting the electrodes to a hand-held FM radio transmitter or to a Grass P-51 amplifier. When we used the transmitter, the signal was received with a Narco Biosystems Biotelemetry receiver, amplified, filtered, and recorded on cassette tape. When we used the amplifier, the amplified ECG signal was recorded directly with a portable cassette recorder. Between tests, the electrodes were allowed to trail behind the fish. During recording, an investigator retrieved the electrodes, connected them to the FM transmitter or amplifier, and then followed the fish by walking around the inside of the tank. Care was taken to leave the ECG wires slack but clear of the fins, so as not to interfere with the fish's swimming movements. At the conclusion of the experiment, heart rates (beats per minute, $\mathrm{bt \cdot min^{-1}}$) were measured by playing the cassette tape back through an HP 5308A frequency counter that was connected to an IBM AT computer. The frequency counter measured time intervals between approximately every other heart beat, and the computer converted these data to heart rates. Heart rates were averaged over 1-min intervals and then matched to the corresponding measurements of swimming speed and $\mathrm{Pio_2}$ for statistical analysis.

Data were collected over 50-min experimental runs consisting of a 10-min control period, a 30-min hypoxic period, and a 10-min recovery period. About 15 min were required to reach the minimum $\mathrm{Pio_2}$ of 70 mmHg. At the conclusion of the hypoxic period, the tank was returned to full O_2 saturation as quickly as possible. The ECG leads were disconnected from the amplifier or transmitter, and the fish was allowed a 1-h recovery period before the next test. Animals were exposed to no more than two hypoxic trials. No individual was reused in subsequent experiments.

Ventilation Volume Experiment

We measured $\dot{V}_g$ with a continuous infusion dye dilution technique, using one dye infusion and two (left and right side) exhaled water sampling catheters, as described by Bushnell et al. (1990) and Jones et al. (1990). Catheters were implanted under general anesthesia, and the animals were revived in the test tank by pumping fresh seawater over the gills as described in Jones et al. (1986, 1990). Fish were given approximately 2 h to recover before the first hypoxic trial. Six skipjack (fork length, 47.4–49.0 cm; body weight, 1.824–2.019 kg) and eight yellowfin tuna (fork length, 49.4–57.4 cm; body weight, 2.050–4.032 kg) were used.

Separate water samples were taken to determine $\mathrm{Peo_2}$, $\mathrm{Pio_2}$, and dye concentrations. A second Radiometer system, with a water-jacketed electrode maintained at the test-tank temperature, was used to measure $\mathrm{Pio_2}$ and $\mathrm{Peo_2}$. Sampling exhalant water for dye dilution and $\mathrm{Peo_2}$ generally required about 60 s. Water samples were taken and lap times recorded simultaneously. Dye dilution samples were stored and analyzed at the end of the day, whereas $\mathrm{Pio_2}$ and $\mathrm{Peo_2}$ samples were measured immediately. The $\mathrm{Po_2}$ electrodes were recalibrated with air-saturated water before each set of measurements.

The P_{IO_2} was reduced after three sets of control measurements were completed. Samples for $\dot{V}_g$, P_{IO_2}, and P_{EO_2} were taken, and lap times were recorded, as often as possible during the entire hypoxic episode. The minimum P_{IO_2} reached was approximately 90 mmHg. One hour was allowed for recovery between tests. Animals were exposed at most to two hypoxic trials. No individual was reused in subsequent experiments.

Utilization (U, in percent) and $\dot{V}O_2$ ($mg\ O_2 \cdot min^{-1}$) were calculated from measured values:

$$U = [(P_{IO_2} - P_{EO_2})/P_{IO_2}] \times 100,$$

and

$$\dot{V}O_2 = \dot{V}_g \times [(P_{IO_2} - P_{EO_2}) \times \alpha],$$

where α is the solubility of O_2 in seawater ($mg \cdot L^{-1} \cdot mmHg^{-1}$) and $\dot{V}_g$ is in $L \cdot min^{-1}$.

Data Reduction and Statistical Procedures

An unpaired Student's *t*-test was used to compare mean control (i.e., normoxia) P_{IO_2}, P_{EO_2}, HR, swimming speed, $\dot{V}_g$, U, and $\dot{V}O_2$ between the two species and to compare data from swimming fish with those from spinally blocked tunas reported in Bushnell et al. (1990).

Because the large volume of water in the test tank precluded step changes in P_{IO_2}, data recorded during hypoxia were divided into P_{IO_2} ranges (>150, 149–130, 129–110, 109–90, and 89–70 mmHg). To reduce variability between fish, percent changes from control means were determined. Mean (± standard error of the mean, SEM) percent changes in P_{IO_2}, HR, swimming speed, $\dot{V}_g$, U, and $\dot{V}O_2$ were calculated for each range.

To determine at what level of hypoxia swimming speed and HR became significantly different from control measurements, a "breakpoint P_{IO_2}" was calculated for each experimental run. This was done by calculating 95% confidence intervals for mean swimming speed and HR in normoxia and comparing those to swimming speed and HR during hypoxia. The breakpoint P_{IO_2} swimming speed was taken to be the P_{IO_2} at which swimming speed exceeded the upper limit of the 95% confidence interval of mean control swimming speed. Similarly, the breakpoint P_{IO_2} for HR was the P_{IO_2} at which HR was significantly lower than the lower limit of the 95% confidence interval of mean control HR. In general, in the heart rate experiments, once swimming speed began to increase and HR began to decrease, they continued to do so. In a few cases, inconsistent changes in HR, swimming speed, or both were observed during hypoxia. These animals were eliminated from the breakpoint analysis. Grand mean breakpoints for HR and swimming speed were calculated by combining data from all skipjack tuna or all yellowfin tuna.

Results

Heart Rate Experiment

Table 1 summarizes the data collected from skipjack and yellowfin tunas in normoxia. The only significant difference was in absolute mean swimming speed, which was higher in skipjack tuna. As for the effect of swimming speed on HR, only four yellowfin tuna showed enough variability in speed during normoxia to provide usable data. As shown in figure 1, higher swimming speeds are associated with higher HR. (Note that some swimming

TABLE 1

Summary of normoxic (control) values (± SEM) measured in swimming yellowfin and skipjack tunas during the heart rate experiment

Variable	Yellowfin Tuna	Skipjack Tuna
Mass (kg)	1.9 ± .5 (6)	1.3 ± .1 (7)
Fork length (cm)	46.1 ± 4.4 (6)	44.7 ± .5 (7)
Control P_{IO_2} (mmHg)	151.7 ± 1.1 (6)	153.6 ± 1.3 (7)
Heart rate (beats · min^{-1})	67.9 ± 3.4 (6)	76.8 ± 7.0 (7)
Swimming speed:		
$cm \cdot s^{-1}$	52.9 ± 4.1 (6)	73.0 ± 6.1* (6)
Body lengths · s^{-1}	1.2 ± .2 (6)	1.6 ± .1 (6)

Note. Numbers in parentheses are the number of fish from which data were obtained.
* Significant difference ($P < 0.05$) between yellowfin and skipjack tunas.

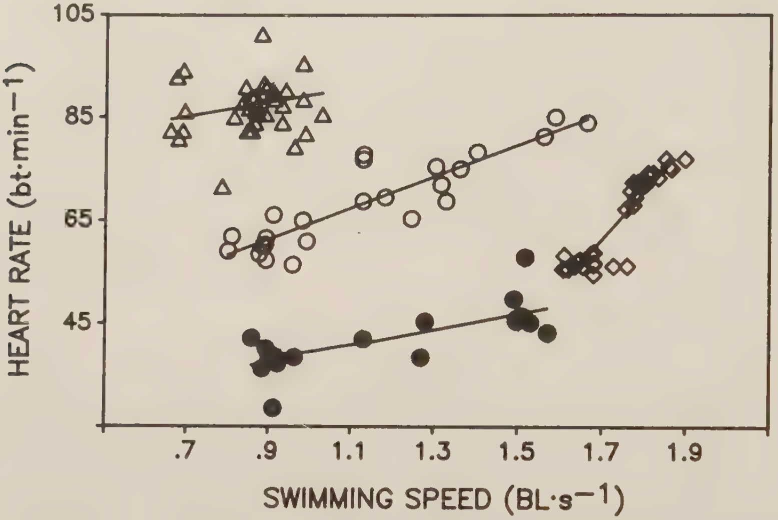

Fig. 1. Effects of voluntary increases in swimming speed on heart rate in four yellowfin tuna during normoxia. Solid lines are least-squares linear regressions.

speeds shown are below the predicted minimum hydrostatic equilibrium swimming speed [Magnuson 1978] for yellowfin tuna. This is most likely due to the fish's adopting a head-up tilting behavior as has been observed in Atlantic mackerel [*Scomber scombrus,* He and Wardle 1986], which, like tuna, are also negatively buoyant.)

The HR of an individual swimming yellowfin tuna is shown in figure 2*A*. The corresponding Pio_2, swimming speeds, and mean HR (averaged over 1-min intervals) are shown in figure 2*B*. The direct effect of hypoxia on swimming speed and heart rate can be clearly seen. All other yellowfin and skipjack tuna similarly tested also had a pronounced bradycardia when exposed to hypoxia. The bradycardia occurred despite concomitant increases in swimming speed, and, initially, heart rates slowed at rates similar to those seen in spinally blocked fish (Bushnell et al. 1990) (fig. 3*A*, *B*). However, when Pio_2 fell below 100 mmHg, the HR leveled off in yellowfin tuna and increased in skipjack tuna.

Breakpoint analyses showed that relatively modest declines in Pio_2 are enough to elicit significant reductions in HR and significant increases in swimming speed in both tuna species. The grand mean (± SEM) breakpoint Pio_2's for heart rate and swimming speed for skipjack tuna were 130.3 (± 7.5) and 123.6 (± 3.1) mmHg, respectively. The grand mean (± SEM) breakpoint Pio_2's for heart rate and swimming speed of yellowfin tuna were 129.9

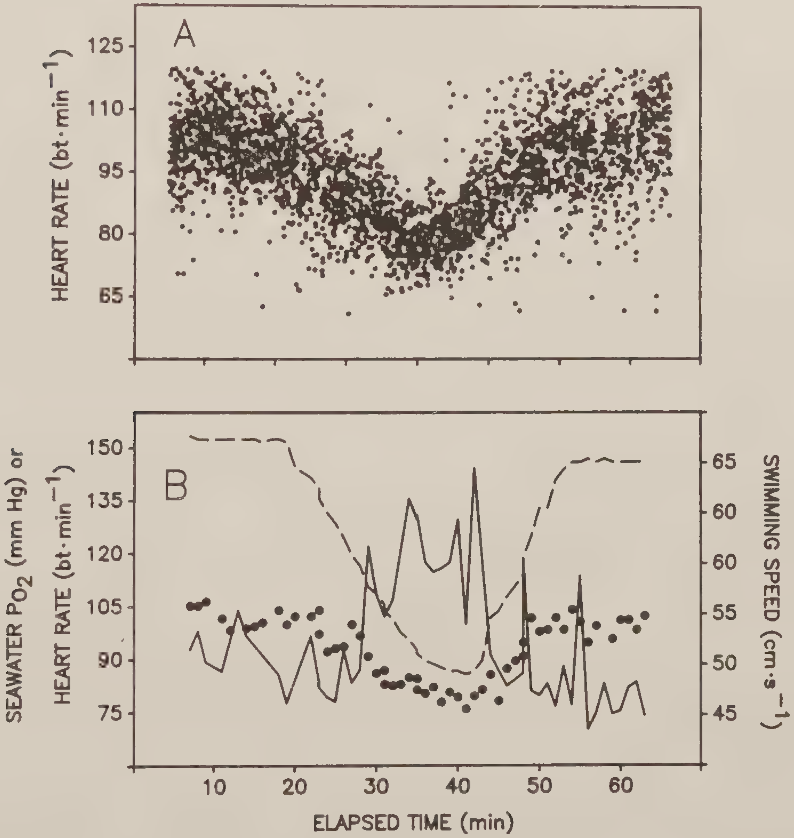

Fig. 2. (A) *The HR of a swimming yellowfin tuna, calculated from the time intervals between approximately every other heart beat; and* (B) *the corresponding* Pio_2 *(broken line), swimming speeds (solid line), and mean (averaged over 1-min intervals) heart rates (filled circles). The direct effect of hypoxia on swimming speed and heart rate can be clearly seen.*

(± 2.0) and 123.8 (± 6.5) mmHg, respectively. These were not significantly different in the two species or from the HR breakpoint Po_2 seen in spinally blocked fish (Bushnell et al. 1990).

Ventilation Volume Experiment

Of the six skipjack tuna used, only four regained the ability to swim at all following anesthesia, and none completed an entire hypoxia trial before losing equilibrium. Therefore, no data were recorded for skipjack tuna in

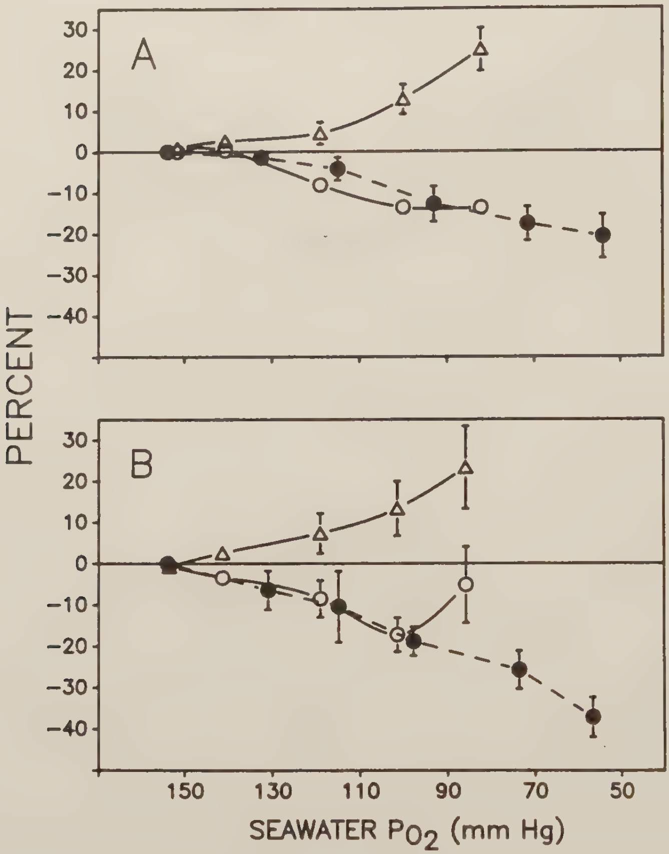

Fig. 3. Effect of hypoxia on relative changes (percent changes from mean values measured during normoxia) in swimming speed (open triangles) and heart rate (open circles) of swimming (A) *yellowfin tuna and* (B) *skipjack tuna. Changes in heart rate in response to hypoxia of spinally blocked yellowfin and skipjack tunas are shown by filled circles (data on spinally blocked tunas are from Bushnell et al.* [*1990*]*).*

hypoxia. In contrast, seven of the eight yellowfin tuna tested completed at least the first hypoxic trial.

With the exception of $\dot{V}O_2$, all variables measured in yellowfin tuna during normoxia were significantly different from those measured in skipjack tuna (table 2). The Pe_{O_2}, weight specific $\dot{V}_g$, and swimming speed were higher in latter; U was lower. Swimming speeds of skipjack tuna were higher during the ventilation volume experiment (2.2 ± 0.2 BL · s^{-1}) than during the heart rate experiment (1.6 ± 0.1 BL · s^{-1}). They were not significantly different in yellowfin tuna, however.

TABLE 2

Summary of mean normoxic control values (± SEM) measured in swimming yellowfin and skipjack tunas during the ventilation volume experiment

Variable	Yellowfin Tuna	Skipjack Tuna
Mass (kg)	2.8 ± .2 (7)	1.8 ± .1* (3)
Fork length (cm)	53.7 ± 1.0 (7)	47.2 ± 1.4* (3)
Pio$_2$ (mmHg)	154.7 ± .9 (7)	152.0 ± 1.2 (3)
Peo$_2$ (mmHg)	67.3 ± 2.6 (7)	85.1 ± 8.1* (2)
Utilization (%)	55.3 ± 2.0 (7)	44.3 ± 5.7* (2)
Ventilation volume:		
L · min^{-1}	8.1 ± 1.1 (7)	10.2 ± 1.4 (3)
L · min^{-1} · kg^{-1}	2.9 ± .4 (7)	5.3 ± 1.0* (3)
Swimming speed:		
cm · s^{-1}	68.0 ± 5.7 (7)	104.2 ± 10.0* (3)
Body lengths · s^{-1}	1.3 ± .1 (7)	2.2 ± .2* (3)
Oxygen consumption (mg O$_2$ · h^{-1} · kg^{-1})	624 ± 65 (7)	1,082 ± 398 (2)

Note. Numbers in parentheses are the number of fish from which data were obtained. Three sets of measurements of Pio$_2$, Peo$_2$, and swimming speed were obtained from each fish.
* Significant difference ($P \leq 0.05$) between yellowfin and skipjack tunas.

Figure 4 shows the changes in swimming speed, $\dot{V}O_2$, U, and $\dot{V}_g$ in swimming yellowfin tuna. For comparison, data on the changes in $\dot{V}_g$ of spinally blocked fish (Bushnell et al. 1990) in response to hypoxia are also plotted. Note that the changes in $\dot{V}_g$, in response to hypoxia, are equivalent and that U decreased as $\dot{V}_g$ increased. Surprisingly, in contrast to the HR experiment,

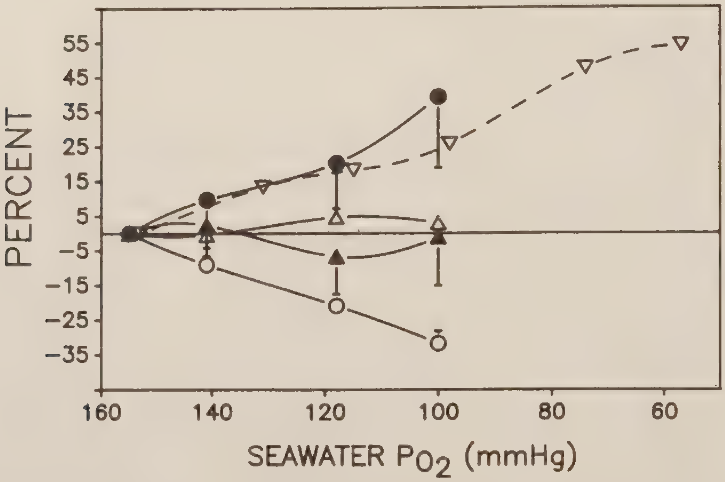

Fig. 4. Effect of hypoxia on relative changes (percent changes from mean values measured during normoxia) in utilization (open circles), ventilation volume (filled circles), swimming speed (open triangles), and oxygen consumption rate (filled triangles) of swimming yellowfin tuna (± SEM). Changes in ventilation volume (inverted triangles) of spinally blocked fish (from Bushnell et al. 1990) are also plotted.

swimming speed did not change. The $\dot{V}O_2$ also remained unchanged throughout the course of hypoxia.

Discussion

Normoxia

The swimming speeds of skipjack and yellowfin tunas in the heart rate experiment, and those of yellowfin tuna in the ventilation volume experiment, were similar to the swimming speeds of the uninstrumented animals used by Dizon (1977). Oxygen consumption rates of yellowfin tuna were comparable to those of the spinally fish used by Bushnell et al. (1990) but were almost double those of uninstrumented tunas studied by Boggs (1984).

Some stress, most likely associated with the general anesthesia required to implant the catheters, appeared to affect skipjack tuna in the ventilation volume experiments. They swam faster than the uninstrumented fish studied by Dizon (1977) and Boggs (1984), although their metabolic rate was not significantly different from those measured by Boggs (1984). Therefore, some anaerobic metabolism may have been involved, and this may explain why they did not survive even mild hypoxia.

There were some significant differences in cardiorespiratory variables measured in swimming yellowfin tuna and those measured in spinally blocked animals by Bushnell et al. (1990). The U in swimming fish (55%) was significantly higher than in spinally blocked fish (39%) but was essentially identical to those of swimming kawakawa (*Euthynnus affinis*) (55%) and swimming yellowfin tuna (56%) measured by Jones et al. (1990). The weight-specific $\dot{V}_g$ of swimming yellowfin tuna was significantly lower than the weight-specific $\dot{V}_g$ of spinally blocked fish (Bushnell et al. 1990). Therefore, spinally blocked yellowfin tuna, although able to set their own ventilation volume, apparently allow themselves to be overventilated. The U and weight-specific $\dot{V}_g$ of swimming skipjack tuna were not significantly higher than those of spinally blocked fish. Unfortunately, the small amount of data on the $\dot{V}_g$ of skipjack tuna, and their high variability, precludes detailed comparisons with spinally blocked fish.

The HR of swimming skipjack and yellowfin tunas were both 34% *lower* than the HR observed in spinally blocked fish (Bushnell et al. 1990) The reasons for this are unknown, but, in yellowfin tuna, this may be due to the apparent overventilation of spinally blocked animals rather than an effect of exercise. The effect of exercise on altering HR in teleost fish is not clear. A review by Jones and Randall (1978) presents evidence for decreases, increases, and no change in HR with exercise. In the four yellowfin tuna that, in normoxia, swam over a range of speeds great enough to show the effects of swimming speed on HR, HR and swimming speed were positively correlated. Moreover, the HR's we observed in swimming tunas were nowhere near the maximum heart rates (250–260 bt $\cdot$ min^{-1}) previously reported for swimming tunas (Kanwisher, Lawson, and Sundnes 1974) or for tunas paralyzed with a neuromuscular blocking agent and artificially ventilated (Brill 1987).

Hypoxia

Most previous studies measuring changes in swimming speeds of fish exposed to hypoxia used species capable of pumping water over their gills, and behavioral responses to hypoxia were found to depend on the experimental paradigm. For example, restrained dogfish sharks (*Scyliorhinus canicula*) became more active when exposed to hypoxia (Randall 1970), whereas unrestrained animals either became less active or remained inactive (Metcalf and Butler 1984). However, most fish reduce their activity during hypoxia (Randall 1970), presumably to reduce O_2 demand. Because tunas are obligate ram ventilators (Roberts 1978), this option has severe limitations. A decrease in speed would reduce $\dot{V}_g$ unless there were a concomitant increase in mouth gape (i.e., mouth cross-sectional area). Although an increase in swimming speed is energetically expensive, it may be necessary if an increase in gape is not effective in maintaining O_2 delivery (this concept is more fully explored in the following sections where we expand Dizon's [1977] mathematical model of O_2 delivery in tunas). Examples of both kinds of responses were seen in this study. In the HR experiment, both species increased swimming speed in response to decreases in P_{IO_2}. However, in the $\dot{V}_g$ experiment, yellowfin tuna increased their speed by an average of only 4%. Since $\dot{V}_g$ increased by 40%, these fish must have increased gape (and possibly also opercular flare). Moreover, the increases in $\dot{V}_g$ in swimming and spinally blocked yellowfin tuna (Bushnell et al. 1990) are essentially identical, indicating the suitability of the former technique for studying the responses and tolerances of tunas to hypoxia.

When compared with the uninstrumented fish used by Dizon (1977), the tunas in our HR study displayed a higher sensitivity to hypoxia. In other words, the P_{IO_2} at which they evinced an increase in swimming speed was higher. The breakpoint P_{IO_2} for swimming speed in *both* tuna species used in our study (ca. 124 mmHg) is higher than the 100 mmHg that Dizon (1977) reported as necessary to elicit swimming-speed changes in skipjack tuna.

As stated previously, Dizon (1977) found that yellowfin tuna did not increase swimming speed even when they were exposed to severe hypoxia. This is perplexing since his and our studies were conducted in the same tank with the same water system, using similarly sized fish, which, in normoxia, swam at identical swimming speeds. The major differences between protocols were that our fish towed ECG wires and were exposed to hypoxia much more rapidly. In Dizon (1977), the time required to go from normoxia to hypoxia ($P_{IO_2} \approx 70$ mmHg) and back to normoxia was approximately three times longer than in our study. The rate at which hypoxia deepens has been shown to be important in determining physiological responses in other fishes (Butler and Taylor 1971). Whether this is an important factor in the responses of tunas to hypoxia remains to be determined.

In swimming skipjack and yellowfin tunas exposed to hypoxia, HR appears to be influenced by two opposing drives: hypoxia and exercise. Initially, as P_{IO_2} falls, the hypoxia response dominates, because swimming speed has not yet increased very much. When P_{IO_2} has fallen enough to generate about a 10% increase in swimming speed, HR stops falling in yellowfin tuna and increases in skipjack tuna. At this point, the exercise drive to increase HR appears to begin to dominate. Regardless of this, the equivalent fall in HR in spinally blocked and swimming tunas clearly demonstrates the utility of the former technique for elucidating the responses to and tolerances of tunas to hypoxia. The inability of spinally blocked tunas to swim does not appear to affect the HR response until severe levels of hypoxia are reached.

Model of O_2 Delivery in Tunas

Dizon (1977) created a mathematical model predicting the relationship among swimming speed, gape, O_2 demand, and O_2 delivery in skipjack tuna during normoxia and hypoxic. His results are replotted in figure 5*A*, *B*.

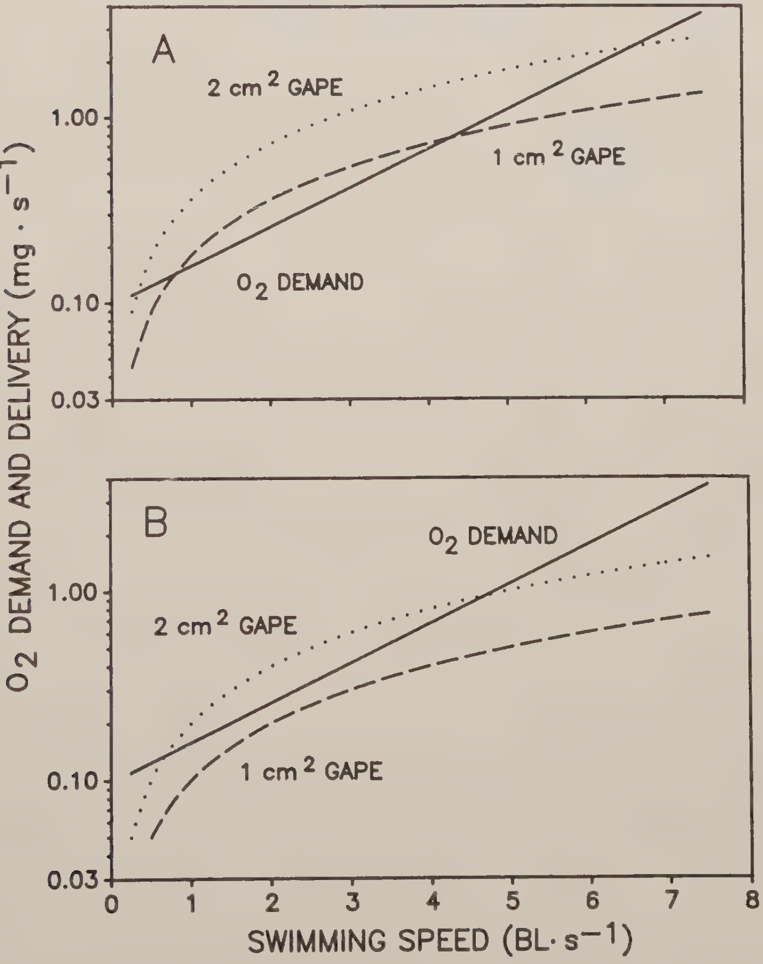

Fig. 5. Dizon's (1977) model of oxygen demand and effects of gape (i.e., mouth cross-sectional area) on oxygen delivery in skipjack tuna in (A) *normoxia and* (B) *hypoxia. In this model, hypoxia is defined as a sea-water Po_2 = 85 mmHg.*

Since the model predicts that O_2 delivery rises linearly with speed and O_2 demand rises exponentially, a point is reached where O_2 demand exceeds delivery. Beyond this (the maximum aerobic swimming speed), further metabolic needs must be met anaerobically. During normoxia, the maximum aerobic swimming speed predicted by Dizon's (1977) model for a 40-cm fork length (1.4 kg) skipjack tuna is 4.5 $BL \cdot s^{-1}$ with a 1-cm^2 gape (dotted line, fig. 5*A*) and 6.5 $BL \cdot s^{-1}$ with a 2-cm^2 gape (dashed line, fig. 5*A*). Hypoxia is predicted to shift both O_2 delivery lines down (fig. 5*B*), such that oxygen delivery with a 1-cm^2 gape is below O_2 demand at all swimming speeds. His model therefore predicts that, during hypoxia, O_2 demand must be met by increasing gape rather than by increasing swimming speed alone.

Dizon's (1977) model contains two important parameters that we now know to be incorrect: (1) that O_2 consumption increases exponentially with swimming speed and (2) that U remains at 75% (i.e., U is independent of $\dot{V}_g$). The former was based on data given in Gooding, Neill, and Dizon (1981), and the latter on data provided in Stevens (1972). We therefore decided to reanalyze Dizon's (1977) model incorporating the following: data on swimming speed and metabolic rate provided by Boggs (1984) and Olson and Boggs (1986) and data on the effects of swimming speed on $\dot{V}_g$ and the effects of $\dot{V}_g$ and PiO_2 on U developed in the present study. We also decided to extend the model to include yellowfin tuna. All of the assumptions and specific equations used in our model are given in the Appendix.

Incorporating the relationships for U, $\dot{V}_g$, $\dot{V}O_2$, PiO_2, and swimming speed described in the Appendix results in a model with several noteworthy features (figs. 6, 7). As in Dizon's (1977) model (fig. 5), the slowest speeds that skipjack and yellowfin tunas can swim are predicted to be unconstrained by O_2 delivery. Oxygen delivery clearly exceeds demand even at speeds well below predicted minimum hydrostatic equilibrium swimming speeds (Magnuson 1973). The predicted maximum aerobic swimming speeds in normoxia are 5.6 and 3.5 $BL \cdot s^{-1}$ for yellowfin and skipjack tunas, respectively. Doubling the gape in normoxia (fig. 6) slightly increases the maximum aerobic swimming speed of skipjack tuna but reduces that of yellowfin tuna. This is a result of the reduction in U that is predicted at the higher $\dot{V}_g$. Maximum predicted $\dot{V}O_2$ at these speeds equaled 2,469 and 2,700 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$ (0.96 and 1.05 mg $O_2 \cdot s^{-1}$) in yellowfin and skipjack tunas, respectively; these values are close to the maximum $\dot{V}O_2$ measured in freshly caught skipjack tuna (2,500 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$; Gooding et al. 1981) and are roughly three times the maximum $\dot{V}O_2$ of other teleosts (1,000 ± 200 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$; Brett 1972).

The maximum aerobic swimming speeds predicted by our model are quite high for most teleosts but appear low in light of the reputation of tunas for prolonged, high-speed swimming. Beamish (1978), for instance, cites an example of a 40-cm skipjack tuna swimming at 20 BL · s^{-1} for 3 h. Anecdotal evidence from fishermen and others implies that schools of skipjack and yellowfin tunas are capable of swimming speeds in excess of 7–8 BL · s^{-1} for days. However, after reviewing documented tuna swimming speeds (Yuen 1970; Dizon 1977; Dizon, Brill, and Yuen 1978; Magnuson 1978; Gooding et al. 1981; Carey and Olson 1982; Boggs 1984; Holland, Brill, and Chang 1990), we found that, when swimming speeds surpass the maximal sustainable speeds predicted by our model, they always occurred for less than 200 min and therefore probably involved some degree of anaerobic metabolism (Beamish 1978).

In our model doubling gape does not appreciably extend maximum sustainable swimming speeds of skipjack tuna and reduces those of yellowfin tuna because of the concomitant decrease in U. Doubling the gape does, however, increase the O_2 delivery available for lactate metabolism (in fig. 6, the shaded areas between O_2 demand and delivery lines) by 36% in yellowfin tuna and 92% in skipjack tuna. At swimming speeds that are optimal for O_2 debt repayment, the maximum predicted O_2 delivery exceeds metabolic demand by 293%–525% in yellowfin tuna and 285%–393% in skipjack tuna, depending on gape.

In our model, increasing swimming speed during hypoxia (4.0 mg O_2 · L^{-1}, Pio_2 85 mmHg), if unaccompanied by an increase in gape, is predicted to be an ineffective response to hypoxia (fig. 7*A*, *B*). Doubling gape from 1 to 2 cm^2 results in enough oxygen delivery to allow both species to meet their metabolic needs aerobically at swimming speeds of 1.2–1.4 BL · s^{-1}. These velocities are right at the minimum hydrostatic equilibrium swimming speed of yellowfin tuna and substantially below that of skipjack tuna. In other words our model predicts that a Pio_2 of 85 mmHg is close to the minimum survivable O_2 tension for yellowfin tuna and is below the minimum survivable for skipjack tuna.

Even with a doubling of gape, increases in swimming speed beyond 1.2–1.4 BL · s^{-1} during hypoxia are predicted to not increase O_2 delivery. This agrees with experimental observations. When Gooding et al. (1981) exposed skipjack tuna to prolonged (4 h) levels of hypoxia (3.0–4.0 mg O_2 · L^{-1}, Pio_2 66–88 mmHg), all fish that swam between 1.5 and 2.9 BL · s^{-1} died within 20–155 min. The two fish that survived swam at a speed ($\approx$1 BL · s^{-1}) predicted by our model to be sustainable by aerobic metabolism. Presumably these fish were able to swim at speeds below their minimum predicted hydrostatic equilibrium speed by adopting a head-up tilting behavior similar to that observed in Atlantic mackerel (He and Wardle 1986). Although the ability of tunas to swim below their minimum predicted hydro-

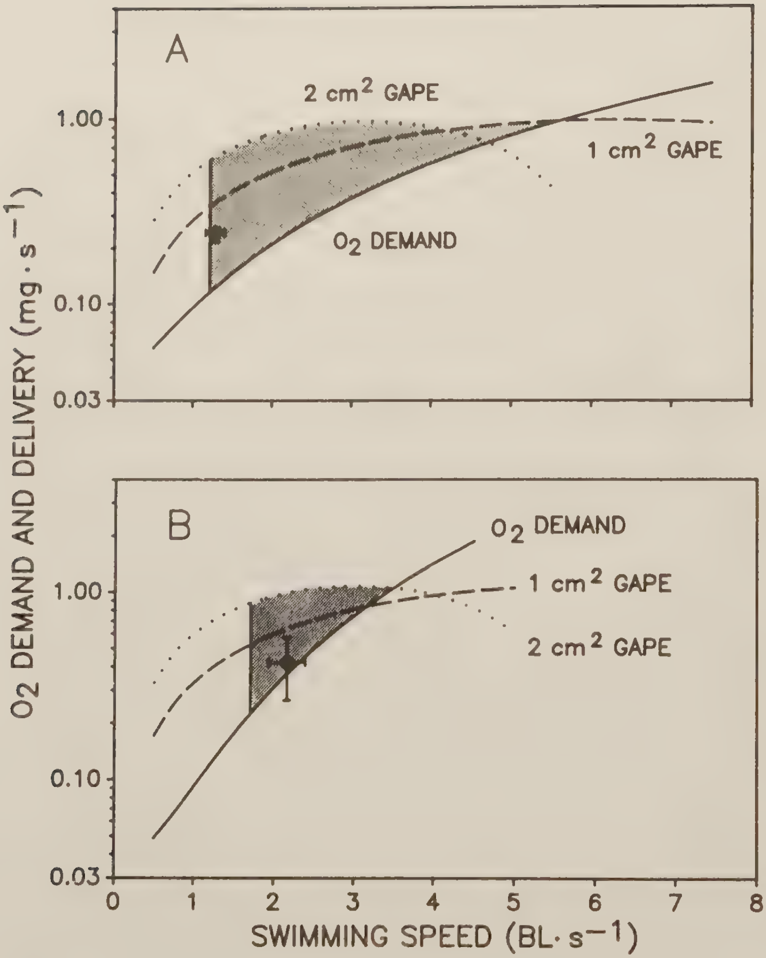

Fig. 6. Revised model of oxygen demand and effects of gape on oxygen delivery in (A) *yellowfin tuna and* (B) *skipjack tuna in normoxia. Note that, because of decreases in utilization, a larger gape (i.e., a higher ventilation volume) does not increase maximum sustainable (i.e., aerobic) swimming speeds. At speeds at which oxygen delivery exceeds demand (shaded areas), fish are capable of repaying oxygen debts. Single data points are the mean (± SEM) oxygen consumption rates and swimming speeds measured in this study during normoxia. Solid vertical lines show minimum hydrostatic equilibrium swimming speeds (from Magnuson 1973).*

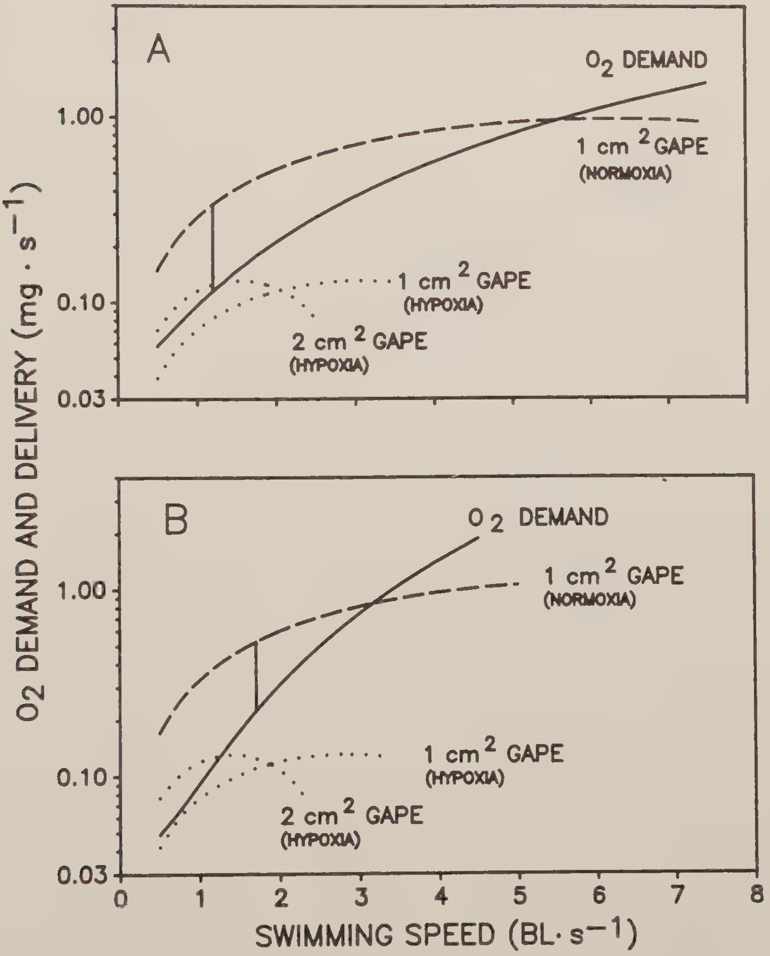

Fig. 7. Revised model of oxygen demand and effects of gape on oxygen delivery in (A) *yellowfin tuna and* (B) *skipjack tuna in normoxia (dashed lines) and hypoxia (dotted lines). Hypoxia in this model is defined as seawater* Po_2 *= 85 mmHg. Solid vertical lines show minimum hydrostatic equilibrium swimming speeds. In yellowfin tuna, a 2-*cm^2 *gape delivers enough oxygen to meet demand, but only at the minimum hydrostatic equilibrium speed, and there is little or no excess oxygen delivery available for repayment of oxygen debts. For skipjack tuna in hypoxia, even with a 2-*cm^2 *gape, oxygen delivery is well below oxygen demand at all speeds above minimum hydrostatic equilibrium speed.*

static equilibrium speeds makes prediction of lethal O_2 levels somewhat difficult, it is obvious that fish that must adopt these behaviors would not have the O_2 delivery capacity necessary to metabolize the high levels of white-muscle lactate known to be generated in feeding fish (Hochachka, Hulbert, and Guppy 1978). In other words, O_2 levels this low would not be survivable for prolonged periods.

The increases in swimming speeds in response to hypoxia observed in skipjack and yellowfin tunas in the HR portion of our study and in skipjack tuna in Dizon (1977) therefore are most likely a flight response. In other words increased swimming speed appears to be a behavior whose objective is to move the fish out of the hypoxic water, rather than an attempt to deliver enough O_2 to meet metabolic demand.

The picture of tuna swimming performance that results from our study and modeling efforts contradicts the currently held view that tunas are capable of very high, sustained speeds (Stevens and Dizon 1982). Tunas appear to be capable of high average swimming speeds—not as a consequence of an unusually large relative aerobic scope—but because a large glycolytic capacity is paired with an ability to repay O_2 debts at swimming speeds that are still quite high when compared with most teleosts. Furthermore, the capacity to provide large amounts of O_2 to the gills appears to be only one of several physiological adaptations for quick recovery from anaerobic exercise (Barrett and Connor 1964; Moon et al. 1986; Weber, Brill, and Hochachka 1986; Brill 1987). For example, studies by Perry et al. (1985) show that skipjack tuna can compensate for a 0.4-unit decrease in arterial blood pH (resulting from exhaustive exercise) within 30 min and that they can clear the metabolic proton load within 50 min. In other teleosts, these processes take 24 h or longer (Jones and Randall 1978).

Acknowledgments

We thank Mark Ablondi, Robert Bourke, and Cheryl Watson for their assistance in performing the experiments; Andrew Dizon, Pierre Kleiber, and E. Don Stevens for reviewing early drafts of the manuscript; and Leslie Williams for extensive editorial help. We also thank Robert Furrilla for providing the hand-held FM radio transmitters. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, National Oceanic and Atmospheric Administration.

Appendix

To make the results of our model directly comparable to those of Dizon (1977), we also base our model 40-cm fork length (1.4-kg) fish and 24°C seawater containing 7.2 mg $O_2 \cdot L^{-1}$ at full saturation ($Pio_2 = 154$ mmHg). Hypoxia is defined as $Pio_2 = 85$ mmHg or 4.0 mg $O_2 \cdot L^{-1}$.

Oxygen Demand

Extensive studies by Boggs (1984) and Olson and Boggs (1986) show that, in tunas, $\dot{V}o_2$ (i.e., O_2 demand) is a power function, not an exponential function of speed, as presumed by Dizon (1977). Therefore, in our model, predicted energy demands are reduced at low swimming speeds (<2 BL $\cdot$ s^{-1}) but increase dramatically at moderately higher speeds (>3.8 BL $\cdot$ s^{-1}) when compared to Dizon's (1977) model. Equations 1 and 2 (from Boggs [1984]) also show that energy demands (PWR, W $\cdot$ g^{-1}) of yellowfin (eq. [1]) and skipjack (eq. [2]) tunas decrease exponentially with fork length (FL, cm), are independent of weight (WT, g), and (as stated) increase exponentially with swimming speed (SPD, cm $\cdot$ s^{-1}):

$$\mathrm{PWR} = (4.45 \times 10^{-4} \times \mathrm{WT}^{0.0}) + (1.59 \times 10^{-4} \times \mathrm{SPD}^{1.64} \times \mathrm{FL}^{-1.28}), \qquad (1)$$

and

$$\mathrm{PWR} = (4.26 \times 10^{-4} \times \mathrm{WT}^{0.0}) + (0.91 \times 10^{-4} \times \mathrm{SPD}^{2.36} \times \mathrm{FL}^{-1.86}). \qquad (2)$$

For use in our model, PWR was converted to O_2 demand (mg $O_2 \cdot s^{-1}$) by multiplying the former by body weight (1,400 g) and by 0.0654 mg $O_2 \cdot s^{-1} \cdot W^{-1}$ (Dejours 1975).

Oxygen Delivery

Predicted $\dot{V}o_2$ is a product of $\dot{V}_g$, O_2 content of the water ($[O_2]$, mg $\cdot$ L^{-1}), and U (expressed as decimal fraction):

$$\dot{V}o_2 = \dot{V}_g \times [O_2] \times U. \qquad (3)$$

In our model, $\dot{V}_g$ is a function of swimming speed and gape (i.e., mouth cross-sectional area), and U, in turn, is dependent on $\dot{V}_g$ and Pio_2.

Ventilation Volume

Because we could not control activity, we were unable to measure $\dot{V}_g$ over a wide range of swimming speeds. Therefore, we used mean $\dot{V}_g$ and swimming speeds (table 1) and assumed, like Dizon (1977), that $\dot{V}_g$ is directly proportional to speed. The resulting equations (4) and (5) (yellowfin and skipjack tuna, respectively) relating $\dot{V}_g$ and swimming speed are:

$$\dot{V}_g = 0.052 \times SPD', \tag{4}$$

and

$$\dot{V}_g = 0.057 \times SPD', \tag{5}$$

where SPD′ is swimming speed expressed in BL · s^{-1}. Because there are no measurements of mouth cross-sectional areas of swimming tunas, we assume that equations (4) and (5) are measured in tunas with a 1-cm^2 mouth cross-sectional area. We also assume, as did Dizon (1977), that $\dot{V}_g$ is directly proportional to mouth cross-sectional area. Also, based on data presented in Bushnell et al. (1990), we assume that both species are capable of doubling mouth cross-sectional areas from those required to provide adequate ventilation volumes at minimum O_2 demands.

Incorporating mouth cross-sectional area (GAPE) into equations (4) and (5) yields for yellowfin tuna,

$$\dot{V}_g = 0.052 \times SPD' \times GAPE, \tag{6}$$

and for skipjack tuna,

$$\dot{V}_g = 0.057 \times SPD' \times GAPE. \tag{7}$$

Utilization

Our measurements show that Dizon's (1977) predicted $\dot{V}_g$ for skipjack tuna is approximately 70% too low and that a 75% U is too high. The 75% U, measured by Stevens (1972) in skipjack tuna and used by Dizon (1977), was made in fish artificially ventilated at one-half the normal $\dot{V}_g$ of swimming animals. Data presented here also show that U is not fixed but is dependent on Pio_2 and $\dot{V}_g$ (fig. 4). Similar results have been reported for a variety of other teleosts and elasmobranchs (Saunders 1962; Hanson and Johansen 1970; Bushnell 1982). In our model, a fixed U is therefore replaced by a U that decreases with increasing $\dot{V}_g$ and decreasing Pio_2; the exact relationship was determined by a multiple linear regression of U on $\dot{V}_g$ and Pio_2 using data from yellowfin tuna. Because skipjack tuna did not survive during our attempts to measure $\dot{V}_g$ during hypoxia, the same regression equation is used for both species. Using the same regression equation appears reasonable since the U predicted for skipjack tuna by the multiple linear regression equation for yellowfin tuna is within 1% of the mean U measured in normoxia in spinally blocked and swimming skipjack tuna.

Using the data collected on yellowfin tuna in normoxia and hypoxia in a multiple linear regression of U on $\dot{V}_g$ (L · s^{-1}) and Pio_2 yields

$$U = (Pio_2 \times 0.0029) - (\dot{V}_g \times 1.27) + 0.162, \quad r^2 = 0.50. \tag{8}$$

Tuna have a tremendous anaerobic capacity and can generate white-muscle lactate levels of 70–90 μmol · g^{-1} (Hochachka et al. 1978). To metabolize lactate, tuna must deliver O_2 to the tissues at rates that exceed their usual metabolic demand. We believe that tuna are therefore capable of higher U than those shown by our data, when extra quantities of O_2 are needed to metabolize lactate. Higher U could be achieved by increasing effective gas exchange area of the gills (via lamellar recruitment) and by changes in intralamellar blood flow. Although these have never been demonstrated in tuna, both processes have been shown to be effective in increasing U in other teleosts (Nilsson 1986).

Maximum U and $\dot{V}o_2$ were incorporated into the model by increasing the intercept of equation (8) to achieve a U of 0.75 (i.e., 75%) at the $\dot{V}_g$ predicted to occur at minimum hydrostatic equilibrium swimming speeds of 1.4-kg skipjack and yellowfin tunas (0.097 and 0.062 $L \cdot s^{-1}$ at 1.7 and 1.2 $BL \cdot s^{-1}$, respectively). Substituting normoxic Pio_2 (154 mmHg) and incorporating predicted $\dot{V}_g$ for both species (from eqq. [6] and [7]) yield for yellowfin tuna,

$$U = (Pio_2 \times 0.0029) - (\dot{V}_g \times 1.27) + 0.383, \tag{9}$$

and, for skipjack tuna,

$$U = (Pio_2 \times 0.0029) - (\dot{V}_g \times 1.27) + 0.427. \tag{10}$$

The assumptions made to forecast U in hypoxia were relatively simple. We assume that tunas in this environment maximize their O_2 delivery and are incapable of repaying O_2 debts. Therefore, the U predicted by the multiple linear regression of U on $\dot{V}_g$ and on Pio_2 (eq. [8]) is presumed to represent the highest U of which the fish are capable.

Literature Cited

Barkley, R. A., W. H. Neill, and R. M. Gooding. 1978. Skipjack tuna, *Katsuwonus pelamis,* habitat based on temperature and oxygen requirements. Fishery Bull. U.S. 76:653–662.

Barrett, I., and R. A. Connor. 1964. Muscle glycogen and blood lactate in yellowfin tuna, *Thunnus albacares,* and skipjack tuna, *Katsuwonus pelamis,* following capture and tagging. Inter-American Trop. Tuna Commission Bull. 9:219–268.

Beamish, F. W. H. 1978. Swimming capacity. Pages 101–107 in W. S. Hoar and D. J. Randall, eds. Fish physiology. Vol. 7. Academic Press, New York.

Boggs, C. H. 1984. Tuna bioenergetics and hydrodynamics. Ph.D. diss. University of Wisconsin, Madison. 189 pp.

Brett, J. R. 1972. The metabolic demand for oxygen in fish, particularly salmonids, and a comparison with other vertebrates. Respir. Physiol. 14:151–170.

Brill, R. W. 1987. On the standard metabolic rates of tropical tunas, including the effect of body size and acute temperature change. Fishery Bull. U.S. 85:25–35.

Bushnell, P. G. 1982. Respiratory and circulatory adjustments to exercise in the lemon shark, *Negaprion brevirostris* (Poey). M.S. thesis. University of Miami. 90 pp.

Bushnell, P. G., R. W. Brill, and R. W. Bourke. 1990. Cardiorespiratory responses of skipjack tuna (*Katsuwonus pelamis*), yellowfin tuna (*Thunnus albacares*), and bigeye tuna (*T. obesus*), to acute reductions in ambient oxygen. Can. J. Zool. (in press).

Butler, P. J., and E. W. Taylor. 1971. Response of the dogfish (*Scyliorhinus canicula* L.) to slowly induced and rapidly induced hypoxia. Comp. Biochem. Physiol. 39A: 307–323.

Carey, F. G., and R. J. Olson. 1982. Sonic tracking experiments with tunas. Inter-American Trop. Tuna Commission Spec. Rep. 2:458–446.

Chang, R. K. C., R. W. Brill, and H. O. Yoshida. 1983. The Kewalo Research Facility, 1958–1983—25 years of progress. Southwest Fisheries Center Administrative Report H-83-14, 28 pp. Southwest Fisheries Science Center Honolulu Laboratory, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Honolulu, Hawaii.

Dejours, P. 1975. Principles of comparative respiratory physiology. Elsevier, New York. 251 pp.

Dizon, A. E. 1977. The effect of dissolved oxygen concentration and salinity on swimming speed of two species of tunas. Fishery Bull. U.S. 75:649–653.

Dizon, A. E., R. W. Brill, and H. S. H. Yuen. 1978. Correlations between environment, physiology, and activity and the effects on thermoregulation in skipjack tuna. Pages 233–269 in G. D. Sharp and A. E. Dizon, eds. The physiological ecology of tunas. Academic Press, New York.

Gooding, R. G., W. H. Neill, and A. E. Dizon. 1981. Respiration rates and low-oxygen tolerance limits in skipjack tuna, *Katsuwonus pelamis*. Fishery Bull. U.S. 79:31–47.

Hanamoto, E. 1987. Effect of oceanographic environment on bigeye tuna distribution. Bull. Jpn. Soc. Fisheries Oceanography 51:203–215.

Hanson, D., and K. Johansen. 1970. Relationship of gill ventilation and perfusion in the Pacific dogfish, *Squalus suckleyi*. J. Fisheries Res. Board Can. 27:561–564.

He, P., and C. S. Wardle. 1986. Tilting behavior of the Atlantic mackerel, *Scomber scombrus*, at low swimming speeds. J. Fish Biol., suppl. A, 29:223–232.

Hochachka, P. W., W. C. Hulbert, and M. Guppy. 1978. The tuna power plant and furnace. Pages 153–175 in G. D. Sharp and A. E. Dizon, eds. The physiological ecology of tunas. Academic Press, New York.

Holland, K. N., R. W. Brill, and R. K. C. Chang. 1990. Horizontal and vertical movements of yellowfin and bigeye tunas associated with fish aggregating devices. Fishery Bull. U.S. 88:493–507.

Ingham, M. C., S. K. Cook, and K. A. Hausknecth. 1977. Oxygen characteristics and skipjack tuna distribution in the southeastern tropical Atlantic. Fishery Bull. U.S. 75:857–865.

Jones, D. R., R. W. Brill, P. Butler, P. G. Bushnell, and M. R. A. Heieis. 1990. Measurement of ventilation volume in swimming tunas. J. Exp. Biol. 149:491–498.

Jones, D. R., R. W. Brill, and D. C. Mense. 1986. The influence of blood gas properties on gas tensions and pH of ventral and dorsal aortic blood in free-swimming tuna, *Euthynnus affinis*. J. Exp. Biol. 120:201–213.

Jones, D. R., and D. J. Randall. 1978. The respiratory and circulatory system during exercise. Pages 425–501 in W. S. Hoar and D. J. Randall, eds. Fish physiology. Vol. 7. Academic Press, New York.

Kanwisher, J., K. Lawson, and G. Sundnes. 1974. Acoustic telemetry from fish. Fishery Bull. U.S. 72:251–255.

Magnuson, J. J. 1969. Digestion and food consumption by skipjack tuna *Katsuwonus pelamis*. Trans. Am. Fisheries Soc. 98:379–392.

———. 1973. Comparative study of adaptations for continuous swimming and hydrostatic equilibrium of scombrid and xiphoid fishes. Fishery Bull. U.S. 71:337–356.

———. 1978. Locomotion by scombrid fishes: hydromechanics, morphology, and behavior. Pages 240–308 in W. S. Hoar and D. J. Randall, eds. Fish physiology. Vol. 7. Academic Press, New York.

Metcalf, J. D., and P. J. Butler. 1984. Changes in activity and ventilation response to hypoxia in unrestrained, unoperated dogfish (*Scyliorhinus canicula* L.). J. Exp. Biol. 108:411–418.

Moon, T. W., R. W. Brill, P. W. Hochachka, and J.-M. Weber. 1986. L(+)Lactate translocation into the red blood cells of skipjack tuna, *Katsuwonus pelamis*. Can. J. Zool. 65:2570–2573.

Nakamura, E. L. 1972. Development and uses of facilities for studying tuna behavior. Pages 245–277 in H. E. Winn and B. L. Olla, eds. Behavior of marine animals: current perspectives in research. Vol. 2. Vertebrates. Plenum, New York.

Nilsson, S. 1986. Control of gill blood flow. Pages 86–102 in S. Nilsson and S. Holmgren, eds. Fish physiology: recent advances. Croom Helm, Dover.

Olson R. J., and C. H. Boggs. 1986. Apex predation by yellowfin tuna (*Thunnus albacares*): indirect estimates from gastric evacuation and stomach contents, bioenergetics, and cesium concentrations. Can. J. Fisheries Aquatic Sci. 43:1760–1775.

Perry, S. F., C. Daxboeck, B. Emmett, P. W. Hochachka, and R. W. Brill. 1985. Effects of exhausting exercise on acid-base regulation in skipjack tuna (*Katsuwonus pelamis*) blood. Physiol. Zool. 58:421–429.

Queenth, M. K. K., and R. W. Brill. 1983. Operations and procedures manual for visiting scientists at the Kewalo Research Facility. Southwest Fisheries Center Administrative Report H-83-7, 16 pp. Southwest Fisheries Science Center Honolulu Laboratory, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Honolulu, Hawaii.

Randall, D. J. 1970. The circulatory system. Pages 133–168 in W. S. Hoar and D. J. Randall, eds. Fish physiology. Vol. 4. Academic Press, New York.

Roberts, J. L. 1978. Ram gill ventilation in fish. Pages 83–89 in G. D. Sharp and A. E. Dizon, eds. The physiological ecology of tunas. Academic Press, New York.

Saunders, R. L. 1962. The irrigation of gills in fishes. II. Efficiency of oxygen uptake in relation to respiratory flow activity and concentrations of oxygen and carbon dioxide. Can. J. Zool. 40:817–863.

Sharp, G. D. 1978. Behavioral and physiological properties of tunas and their effects on vulnerability to fishing gear. Pages 397–449 in G. D. Sharp and A. E. Dizon, eds. The physiological ecology of tunas. Academic Press, New York.

Stevens, E. D. 1972. Some aspects of gas exchange in tuna. J. Exp. Biol. 56:809–823.

Stevens, E. D., and A. E. Dizon. 1982. Energetics of locomotion of warm-bodied fish. Annu. Rev. Physiol. 44:121–131.

Sund, P. N., M. Blackburn, and F. Williams. 1981. Tunas and their environment in the Pacific Ocean: a review. Oceanography and Mar. Biol. Annu. Rev. 19:443–512.

Weber, J.-M., R. W. Brill, and P. W. Hochachka. 1986. Mammalian metabolic flux rates in a teleost: lactate turnover in tuna. Am. J. Physiol. 250:R452–R458.

Yuen, H. S. H. 1970. Behavior of skipjack tuna, *Katsuwonus pelamis*, as determined by tracking with ultrasonic devices. J. Fisheries Res. Board Can. 27:2071–2079.

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Mortality and Recruitment of Pacific Sardine, *Sardinops sagax caerulea*, Larvae in the California Current

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Butler, J. L. 1991. Mortality and recruitment of Pacific sardine, *Sardinops sagax caerulea*, larvae in the California Current. Can. J. Fish. Aquat. Sci. 48: 1713–1723.

The mortality rates of Pacific sardine, *Sardinops sagax caerulea*, larvae (<20 d) increased during 1951–67, and this increase was positively correlated with the increase in biomass of northern anchovy, *Engraulis mordax*. Other potential correlates with larval sardine mortality rates were examined using multiple correlation. These included temperature and zooplankton volumes at stations positive for sardine larvae, water column stability, upwelling, transport, salinity anomalies, and Pacific mackerel, *Scomber japonicus*, abundance. None contributed significantly to the multiple regression with anchovy abundance. Thus, no evidence existed for either Lasker's stable ocean hypothesis of larval mortality or Hjort's larval transport hypothesis. The logarithm of the ratio of sardine recruits at age 2 to the spawning biomass was used as an index of recruitment success. Sardine recruitment success at age 2 was not correlated with larval mortality rates. Sardine recruitment, however, was negatively correlated with both northern anchovy biomass and the combined biomass of Pacific sardine, Pacific mackerel, and northern anchovy. A plausible explanation for this result is that predation by pelagic fishes results in greater mortality rates of sardine larvae and juveniles which in turn decrease sardine recruitment.

De 1951 à 1967, les taux de mortalité de larves (< 20d) de sardine du Pacifique (*Sardinops sagax caerulea*) ont montré une augmentation en corrélation positive avec l'augmentation de la biomasse d'anchois du Pacifique (*Engraulis mordax*). L'auteur a utilisé une corrélation multiple pour étudier d'autres facteurs potentiels en corrélation avec les taux de mortalité des larves de sardine, en particulier la température et les volumes de zooplancton présents aux stations fréquentées par des larves de sardine, la stabilité de la colonne d'eau, les remontées d'eau profonde, le transport, les anomalies de la salinité et l'abondance du maquereau (*Scomber japonicus*). Aucun de ces facteurs n'a contribué de façon significative à la régression multiple en fonction de l'abondance de l'anchois. L'hypothèse de l'océan stable de Lasker concernant la mortalité des larves et l'hypothèse du transport des larves de Hjort ne sont donc pas étayées. L'auteur utilise le logarithme du rapport entre le nombre de recrues de sardine de 2 ans et la biomasse de reproducteurs comme indice du succès du recrutement. Le succès du recrutement de sardines de 2 ans n'est pas en corrélation avec les taux de mortalité des larves. Par contre, le recrutement des sardines est en corrélation négative avec la biomasse d'anchois du Pacifique et la biomasse combinée de la sardine, du maquereau et de l'anchois. Une explication plausible de ce résultat serait que la prédation exercée par les poissons pélagiques est la cause de taux de mortalité plus élevés des larves et des juvéniles de sardine, qui ont pour résultat une baisse de son taux de recrutement.

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The causes of larval fish mortality have been the subject of considerable speculation for several decades. Most speculation is on the relative importance of starvation or predation in determining the mortality rate of larvae.

The starvation hypothesis is based in part on the observation that larval fish reared in the laboratory require greater food densities than are generally found in the ocean. Field and laboratory experiments (Hjort 1913, 1926; Lasker 1975) have supported the idea that the availability of food affects the survival of first-feeding larvae. The incidence of starving larvae of northern anchovy, *Engraulis mordax*, and jack mackerel, *Trachurus symmetricus*, in plankton net collections suggests that starvation mortality is restricted to the first 1–2 wk after yolk sac absorption (O'Connell 1980; Hewitt et al. 1985; Theilacker 1986).

The basis of the predation hypothesis is that larval fish are minor constituents of the zooplankton community and that a great many zooplankton and planktivorous fishes eat larval fish. Moreover, eggs and yolk-sac larvae that have internal food supplies and do not die from starvation sustain mortality rates which are greater than first-feeding larvae, and this mortality can be due only to predation (Hunter 1984). Egg and larval predators have been identified in the field, and losses due to predation by copepods (Lillelund and Lasker 1971; Brewer et al. 1984), euphausids (Theilacker and Lasker 1974; Brewer et al. 1984), amphipods (Brewer et al. 1984); jellyfish (Möller 1984; Van der Veer 1985; Purcell et al. 1987), cnidarians and ctenophores (Purcell 1985), and fish (Frank and Leggett 1984; Alheit 1987) have been assessed. Planktivorous fish have been considered to be the cause of as much as 50% of the observed mortality of eggs of the Peruvian anchoveta, *Engraulis ringens* (Alheit 1987).

The objectives of this study were to (1) examine larval mortality rates of the Pacific sardine, *Sardinops sagax caerulea*, population, (2) compare these rates with the mortality rates of northern anchovy during the same period, and (3) investigate interannual variation of larval sardine mortality rates. Three possible hypotheses to explain annual variation in larval sardine mortality rates were investigated. These were the stable ocean hypothesis (Lasker 1978, 1981) which proposes that periods of calm weather are necessary to allow first-feeding larvae to find aggregated food patches, the transport hypothesis (Hjort 1913) which proposes that currents may sweep larvae out of suitable feeding areas, and the predation hypothesis (Hunter 1984) which proposes that the abundance of predators on eggs and larvae will affect mortality rates.

These hypotheses were further tested to determine whether any factor can be used to predict recruitment. The potential predators of eggs and larvae that I considered were adult northern anchovy, Pacific sardine, and Pacific mackerel, *Scomber japonicus*. Jack mackerel were excluded as a potential predator because of their offshore distribution.

Methods

Larval Mortality

I estimated sardine larval mortality rates from the decrease in numbers of larvae in successive size intervals found in 1-m, 500-µm-mesh oblique ring net tows collected by the California Cooperative Oceanic Fisheries Investigation (CalCOFI). Size–frequency distributions of larvae from 3.9 to 16.2 mm were converted to age–frequency distributions using growth rates determined in the laboratory for yolk-sac larvae and in the field for feeding larvae.

Oblique net tows were taken during a series of monthly cruises beginning in 1951 and ending in 1966. Quarterly CalCOFI cruises were initiated in 1961. After 1967 the numbers of sardine larvae collected were insufficient for estimating mortality rates.

Abundance in each length class was estimated using a weighted negative binomial model (Bissell 1972; Zweifel and Smith 1981; Lo 1985). I adjusted the numbers of larvae in ichthyoplankton net collections for the following possible biases: extrusion through the mesh (Lenarz 1972, 1973; Lo 1983), day–night difference in avoidance (Lo 1985), and volume of water filtered at each depth (Kramer et al. 1972).

Duration of yolk-sac stage was determined from temperature-dependent growth rates calculated using the model of Zeifel and Lasker (1976). Sardine larvae hatch 2.24 d after fertilization at 17°C and reach the first-feeding stage in 5 d at a larval length of 6.2 mm (Zweifel and Lasker 1976). As we know from daily increments in their otoliths, sardine larvae reach a length of 15 mm (live standard length) in about 23 d after hatching (Butler and de Mendiola 1985; Castillo et al. 1986; Butler 1987).

Because estimates of the ages of fish larvae stored in formalin for more than 20 yr are unattainable from otoliths, I estimated ages by the duration of each length interval from growth rates back-calculated from increment widths in the otoliths of juveniles hatched in each month of the year (Butler 1987). The daily formation of these increments was demonstrated by Butler and de Mendiola (1985) and Butler (1987). I used a Laird–Gompertz curve to describe the growth rates of larval sardine:

$$(1)\quad L_t = L_\infty\,[L_{ff}/L_\infty]\,e^{-a_m\cdot(t-t_{ff})}$$

where L_t is the live length at age t days from first feeding, L_∞ is the asymptotic length at metamorphosis = 35 mm, L_{ff} is the length at first feeding and first increment formation = 6.2 mm, a_m is the seasonally dependent growth coefficient, and t is the time from first feeding in days or the number of daily increments.

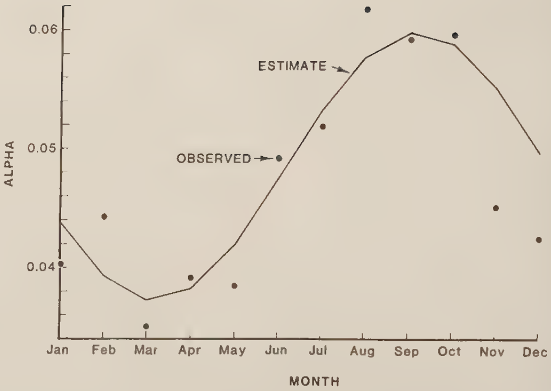

FIG. 1. Seasonal variation in larval growth parameter of the Pacific sardine. Smooth curve is sine function fitted to the data. See text for equation.

I used a sine curve to describe the seasonal growth coefficient (L_m) of the Gompertz curve (Laird 1967):

$$(2)\quad a_m = 0.0485 + 0.00113\cdot\sin(\,(\text{month} - 6.182)\cdot 0.5234).$$

I fitted equation (2) nonlinear regression, weighting the value of alpha of each month by the number of observations for that month (Fig. 1).

Survivorship of sardine larvae increases with age. Survivorship (S) at a given time (t) can be modeled using a Pareto hazard function:

$$(3)\quad S(t) = (t/u)^{-\beta}$$

where u is the time of hatching (Lo 1985). The observed mean daily production of larvae y_i is related to survivorship by

$$(4)\quad y_i = y_u(t/u)^{-\beta}.$$

β was estimated by taking the logarithm of both sides of the equation:

$$(5)\quad \ln(y_i) = B - \beta\ln(t_i/u).$$

Unlike that for anchovy, sardine mortality begins to decline at hatching. I used eight size intervals from hatching to a live size of about 15 mm to estimate β. I compared annual estimates of β for sardine larvae with the annual β for anchovy larvae estimated by Lo (1985) for the same geographic area.

Stable Ocean Hypothesis

To test the stable ocean hypothesis (Lasker 1975, 1981) that larval mortality rates are influenced by stability of the water column, I followed the procedure of Peterman and Bradford (1987), which is to correlate mortality rates with an index of water column stability.

To choose an appropriate stability index, I estimated a geographic center of sardine spawning from the position of positive plankton tows weighted by the number of sardine larvae in each tow. From 1951 to 1967 the latitude of the center of spawning varied from 25°56.4′N in 1965 to 32°11.4′N in 1959, with the overall mean at 28°24.5′N off northern Baja California (Table 1). Since wind data were not available for 29°N, stability indices were calculated from daily average wind speed at

TABLE 1. Geographic distribution of Pacific sardine larvae during 1951–67. Center of distribution is mean position of positive tows weighted by the number of larvae. Southern and northern positions are latitudinal limits of distribution.

	Center		Southern		Northern	
Year	Latitude North	Longitude West	Latitude North	Longitude West	Latitude North	Longitude West
1951	27°52.0′	115°24.7′	22°47.5′	110°22.0′	36°39.0′	122°26.0′
1952	27°59.6′	115°11.1′	24°19.0′	111°48.0′	35°57.0′	119°11.0′
1953	28° 4.3′	115°12.5′	25°33.3′	112°15.5′	34° 9.5′	119°31.8′
1954	29° 8.6′	116° 0.4′	24°21.3′	111°49.0′	35°54.3′	122°22.7′
1955	29°35.6′	116°40.3′	22°35.0′	110°15.1′	34° 8.5′	121° 9.0′
1956	29°10.1′	116° 1.9′	23°55.5′	111° 5.0′	33°47.7′	118°41.0′
1957	29°47.1′	115°55.0′	25°33.5′	112°18.0′	36°39.0′	122°26.0′
1958	31°24.8′	117° 2.4′	24°11.0′	112° 3.0′	36° 9.0′	121°50.0′
1959	32°11.4′	117°50.7′	23°56.0′	111° 4.2′	37°21.0′	124°22.0′
1960	31°10.4′	117°32.4′	24°19.0′	111°48.0′	34°15.2′	119°58.3′
1961	29°31.8′	115°40.6′	25°33.4′	112°18.5′	35°31.7′	121°25.2′
1962	28°27.8′	115°10.9′	26° 4.5′	112°48.0′	36°16.0′	121°40.0′
1963	29°26.1′	115°19.6′	25°38.0′	112°11.2′	36°10.7′	121°45.6′
1964	27°27.9′	113°36.2′	24° 2.0′	113°41.5′	35°38.2′	121°14.2′
1965	25°56.4′	112°27.2′	24°47.4′	112°20.3′	36°54.4′	121°52.9′
1966	27°33.6′	113°31.1′	25°33.6′	112°18.7′	36°10.4′	121°45.9′
1967	29° 0.1′	114°54.0′	25°34.0′	112°19.0′	31°42.1′	116°43.4′

30°N and 116°W. This wind speed index was determined from the number of consecutive 4-d periods of calm weather per month, derived from marine observations from 1953 to 1967.

Based on the analysis of Simpson and Dickey (1981), I used a wind speed of 10 m/s as a cutoff between calm weather and turbulent mixing. Wind speeds greater than 10 m/s produce turbulent mixing in the upper mixed layer which, according to Lasker (1975), should disrupt patches of microzooplankton necessary for successful first feeding of anchovy larvae. The stability index for each month was weighted by the monthly proportion of the annual production of sardine larvae. Missing values of larval production (35 of 204 months) were estimated from adjacent values.

Transport Hypothesis

In the California Current, transport has two components: a southerly component and a seasonal offshore component. To investigate Hjort's hypothesis that transport away from nursery grounds during the larval phase contributes to mortality of larvae, I calculated two indices of transport. Sea level has been shown to be an index of changes in the southerly transport of the California Current (Chelton 1980; Chelton et al. 1982), and offshore Ekman transport is an index of offshore transport (Parrish et al. 1981; Bakun 1985). Each index for each month was weighted by the monthly proportion of the annual production of sardine larvae.

Although no sea level index is available for the center of sardine spawning, the anomalies at one locality are strongly correlated with anomalies at other localities along the coast (Chelton 1980). Thus, the index calculated for San Diego may be considered representative of northern Baja California.

To investigate whether interannual variability in offshore transport influenced the observed increase in larval sardine mortality rates, I calculated an annual index of upwelling at 31°N, 119°W from monthly upwelling indices (Bakun 1973), weighted by the monthly proportion of the annual production of larvae.

Predation Hypothesis

To investigate the hypothesis that the total abundance of coastal pelagic planktivorous fishes affects larval sardine mortality rates, I regressed β on estimates of the total biomass of Pacific sardine by MacCall (1979), Pacific mackerel by Parrish and MacCall (1978), and northern anchovy by Methot (1986). I also regressed β on the biomass estimates of each species. Estimates of total sardine biomass (Table 2) and biomass of recruits at age 2 are from virtual population analysis estimates derived from landings and are independent of the number of sardine eggs and larvae in plankton samples.

The abundance of alternative prey has been proposed to affect the strength of predation by pelagic fish on larval fish (Pepin 1987). To test this hypothesis, I calculated a predator to prey ratio from the total biomass of pelagic fish and zooplankton volumes (Table 3).

To investigate the hypothesis that the abundance of predators affects recruitment through predation on young-of-the-year sardines, I regressed an index of recruitment against the total biomass of coastal pelagic fishes (as defined above) with a 2-yr time lag. The index that I used was the logarithm of the ratio of sardine recruits at age 2 to spawning biomass. Thus, the abundance of predators during the year of spawning was compared with the strength of recruitment 2 yr later. This index was also compared with the biomass of each species to detect any interspecific affects.

Correlation Analyses

Since correlation analysis cannot reveal cause and effect, any correlation may be a result of a correlation with another variable. To test for alternative hypotheses, I performed a stepwise multiple correlation of β and recruitment success on several factors. These factors included temperatures at 10 m (Table 4), zooplankton volumes, latitude of center of spawning, Scripps Pier salinities, sea level anomalies, wind speed indices, upwelling indices, anchovy biomass, Pacific sardine biomass, and Pacific mackerel biomass. Small zooplankton volumes, rou-

TABLE 2. Time series of estimated larval mortality coefficients and total biomass estimates (metric tons, t) of Pacific sardine and northern anchovy during 1951–67.

	Pacific Sardine			Northern anchovy			
Year	Biomass (10^3 t)[a]	Larval β	SE	Biomass (10^3 t)[b]	Larval β	SE	Total biomass (10^3 t)[c]
1951	277	1.74	0.18		0.85	0.15	277
1952	136	2.02	0.25		0.88	0.20	136
1953	202	1.54	0.34		0.95	0.10	202
1954	239	1.77	0.30	45	1.16	0.24	284
1955	170	2.66	0.18	32	1.01	0.17	202
1956	108	2.23	0.33	24	0.88	0.20	131
1957	90	1.65	0.40	88	0.94	0.10	178
1958	177	2.53	0.18	146	0.88	0.08	323
1959	122	2.69	0.18	111	1.18	0.06	233
1960	88	2.35	0.21	66	1.80	0.23	154
1961	54	2.71	0.42	130	1.55	0.16	184
1962	27	2.77	0.36	194	1.08	0.23	221
1963	21	3.79	0.23	204	0.81	0.04	225
1964	11	3.07	0.21	235	1.44	0.21	246
1965	3	3.54	0.28	257	2.42	0.12	260
1966		3.63	0.15	226	1.84	0.04	226
1967		3.77	0.23	195	2.15	0.08	195

[a] From MacCall (1979).
[b] From Methot (1986).
[c] From Lo (1985).

TABLE 3. Annual weighted mean volume of small zooplankton ($cm^3/1000\ m^3$) in 1-m net tows positive for sardine larvae. Mean value weighted by number of sardine larvae collected in tow.

Year	Mean	SD	Low	High
1951	113	63	13	609
1952	154	125	17	1144
1953	168	112	15	1058
1954	145	122	16	1660
1955	209	354	17	6509
1956	289	240	17	1875
1957	165	110	13	2298
1958	110	71	9	532
1959	100	103	7	646
1960	227	164	10	1814
1961	157	93	6	652
1962	164	174	17	1071
1963	382	270	17	1231
1964	225	289	17	1547
1965	372	132	14	977
1966	211	73	17	926
1967	367	272	5	2215

TABLE 4. Annual weighted mean temperature of stations positive for Pacific sardine larvae during 1951–67. Temperature at each station weighted by the number of larvae collected at that station.

	Temperature (°C)					
Year	Mean	Low	High	SD	Stations	Larvae
1951	16.8	11.3	26.4	2.5	162	6059
1952	17.1	11.2	24.4	1.9	203	5512
1953	16.7	12.1	25.2	2.1	175	3414
1954	16.4	12.9	23.7	2.0	355	7108
1955	15.6	12.8	20.2	1.2	255	4358
1956	17.5	11.9	27.4	3.5	169	2692
1957	19.1	13.0	24.8	2.8	173	2712
1958	19.0	11.9	27.3	2.5	193	3824
1959	18.7	12.7	25.0	3.2	170	2079
1960	19.4	10.7	25.0	2.4	138	3723
1961	17.3	12.6	22.0	1.7	53	761
1962	17.7	12.8	23.0	2.2	57	1006
1963	19.7	10.9	24.6	3.2	99	2141
1964	19.6	12.2	25.2	2.9	86	4892
1965	23.2	11.3	26.5	2.0	105	12272
1966	22.4	11.8	24.7	3.2	139	4900
1967	15.7	13.0	20.7	1.8	24	684

tinely measured in the CalCOFI program, are the displacement volumes of the zooplankton taken in ichthyoplankton tows after large gelatinous organisms, such as medusa and salps with individual volumes exceeding 5 mL, are removed (Kramer et al. 1972). These volumes are assumed to be a measure of potential predators rather than larval food which must be collected with 75-μm-mesh nets (Owen et al. 1990).

Temperature, zooplankton volumes, and the geographic positions were weighted by the number of sardine larvae at each station. Weighting produces values representative of the environment experienced by most sardine larvae, but it is not confounded with mortality, which is calculated from abundance of larvae in length classes without regard to their geographic position.

The testing of the significance of correlation coefficients assumes that each observation in the data set is independent. For time series, this requires that the autocorrelation coefficients be small for lag periods greater than zero. This is not the case for time series of populations with generation times greater than the periodicity of sampling. Thus, the time series of anchovy biomass and β are both autocorrelated at a time lag of 1 yr ($R = 0.793$ for anchovy and $R = 0.631$ for β). For autocorrelated time series, Bayley and Hammersley (1946) have proposed a corrected number of independent observations, N^*:

$$(6) \quad 1/N^* = 1/N + 1/N^2 \sum_{j-1}^{N-1} (N-j)\,[P_j\tau]^2$$

where N is the total number of observations and $(P_j T)$ is the autocorrelation coefficient of the j^{th} lag of period. Blackman and Tukey (1958) suggested that j not exceed 1/10 N because of the small number of observations included in the autocorrelations as j approaches $(N-1)$. The significance levels that I use are based on Bayley and Hammersley's (1946) procedure as modified by Blackman and Tukey (1958) (see also Sutcliffe et al. 1976).

Results

Larval Mortality

The log transform for abundance as a function of age is best fit with a straight line (Fig. 2). Thus, the probability of survival of sardine larvae increases with age. The age-specific mortality coefficient, β, varied during 1951–67 (Table 2). The mean value for the 17-yr time series was 2.61 and the variance was 0.562.

Mortality rates of sardine larvae were significantly greater than those of anchovy larvae in the same area in 14 of 17 yr during 1951–67 (Fig. 3). Survival from yolk-sac larvae to 20-mm larvae ranged from 0.05 to 3.1% during 1951–67. During the same period, survival of anchovy larvae from first feeding to 19 mm length ranged from 0.2 to 10.6% (Lo 1985).

Stable Ocean Hypothesis

The estimated mortality rates of sardine larvae showed no relationship to the stability of the water column during 1951–66. There was no significant correlation ($R^2 < 0.03$, $N^* = 14$, $P > 0.37$) with the weighted index of calm weather and the larval sardine mortality coefficient, β.

Salinities of seawater have been correlated with the catch of 3-yr-old Pacific sardine (Walford 1946). This correlation was over a limited time series and attempted to relate the apparent year-class size of Pacific sardine to salinity as an index of upwelling, and hence food availability. Neither larval sardine mortality coefficient, β, calculated here, nor sardine recruitment was correlated with either annual mean Scripps Pier salinities or the annual anomaly from 1951 through 1967 ($R^2 = 0$, $N^* = 14$, $P > 0.10$). Thus, no support was found for the hypothesis that salinity as an index of upwelling affects larval mortality or predicts recruitment.

Transport Hypothesis

Advection of fish larvae away from coastal nursery areas may lead to higher mortality. However, neither the mortality rate of sardine larvae ($R^2 = 0.20$, $N^* = 15$, $P = 0.09$) nor the recruitment of 2-yr-olds ($R^2 = 0.08$, $N^* = 12$, $P = 0.37$) was correlated with the upwelling index at 31°N. Thus, this time series does not support the hypothesis that offshore transport is a determining factor of mortality rates in Pacific sardine larvae.

The mortality rate of sardine larvae showed no correlation ($R^2 = 0.03$, $N^* = 14$, $P > 0.10$) with the sea level anomaly as an index of transport. However, the recruitment of 2-yr-olds showed a positive correlation ($R^2 = 34.3$, $N^* = 13$, $P < 0.05$) with the average sea level anomaly during 1951–67. If the average sea level anomaly is compared with recruitment using a 2-yr time lag, to test the effect of southerly transport during the year that the eggs were spawned, then the correlation is negative, but not significant ($R^2 = 0.074$, $N{:}^* = 13$, $P > 0.10$). Evidence for the hypothesis that southerly transport determines sardine recruitment will be discussed below.

Predation Hypothesis

A corollary of the predation hypothesis is that mortality rates of fish larvae should increase when predator abundance increases. Important predators of planktonic larvae are other zooplankton and planktivorous fish. The mortality of sardine larvae increased in years of high zooplankton volumes (Table 3). Small zooplankton biomass was associated with 36% of the interannual variability of sardine larval β ($N^* = 12$, $P < 0.05$). This indicates a positive relationship between mortality rates and the abundance of zooplankton predators.

Mortality rates of sardine larvae increased over the period 1951–67 (Fig. 3). The biomass of northern anchovy also increased during this period (Table 2). Mortality rates of sardine larvae were positively correlated with anchovy abundance (Fig. 4). The increase in biomass of northern anchovy accounted for 58% of the interannual variability of larval sardine mortality rates ($N^* = 6$, $P < 0.01$).

The abundance of alternative prey affects the strength of fish predation on larval fish. The mortality rate of sardine larvae was positively correlated with the predator prey ratio (pelagic fish biomass/zooplankton volumes) ($R^2 = 0.47$, $N^* = 12$, $P < 0.01$).

Total pelagic fish biomass was significantly negatively correlated with the index of sardine recruit-per-spawn lagged by 2 yr ($R^2 = 0.39$, $N^* = 12$, $P = 0.03$). This correlation is not simply due to a similar time trend in both variables. Pelagic fish biomass varied with a cyclic pattern from 1951 to 1962 (Fig. 5). This time series was significantly negatively autocorrelated at a time lag of 2 yr. The recruitment index of Pacific sardine varied in a similar, but opposite, cycle from 1951 to about 1958. Afterwards, recruitment remained low through 1962.

Biotic factors, rather than abiotic factors, appear to affect larval sardine mortality. The relationship between anchovy biomass and zooplankton biomass seems to explain the observed interannual variability in sardine mortality rates. Larval sardine mortality rates were significantly negatively correlated with both anchovy biomass ($R^2 = 0.63$, $N^* = 8$, $P = 0.001$) and zooplankton biomass ($R^2 = 0.40$, $N^* = 14$, $P = 0.01$). However, larval sardine mortality rates were not correlated with either the total Pacific mackerel biomass ($R^2 = 0.01$, $N^* = 13$, $P > 0.10$) or with the biomass of Pacific mackerel recruits (data from Parrish and MacCall 1978).

The dominant period of the oscillations in pelagic fish biomass (Fig. 5) is 2 yr. This is about the life span of the northern anchovy. To investigate whether northern anchovy affects sardine recruitment, I performed a stepwise multiple correlation analysis on total pelagic fish and anchovy biomass. In this analysis, anchovy biomass was more strongly correlated with sardine recruitment than total pelagic fish biomass ($R^2 = 0.37$, $N^* = 6$, $P = 0.08$). Because of the significant correlation between total pelagic fish biomass and anchovy biomass, it is difficult to separate the two hypotheses that predation by northern anchovy or predation by all pelagic fish on late larvae and juvenile sardines determines recruitment. However, the predation hypothesis is supported by this analysis.

Alternative Hypotheses

The correlations found in the preceding sections may not be due to cause and effect but rather to correlations with some

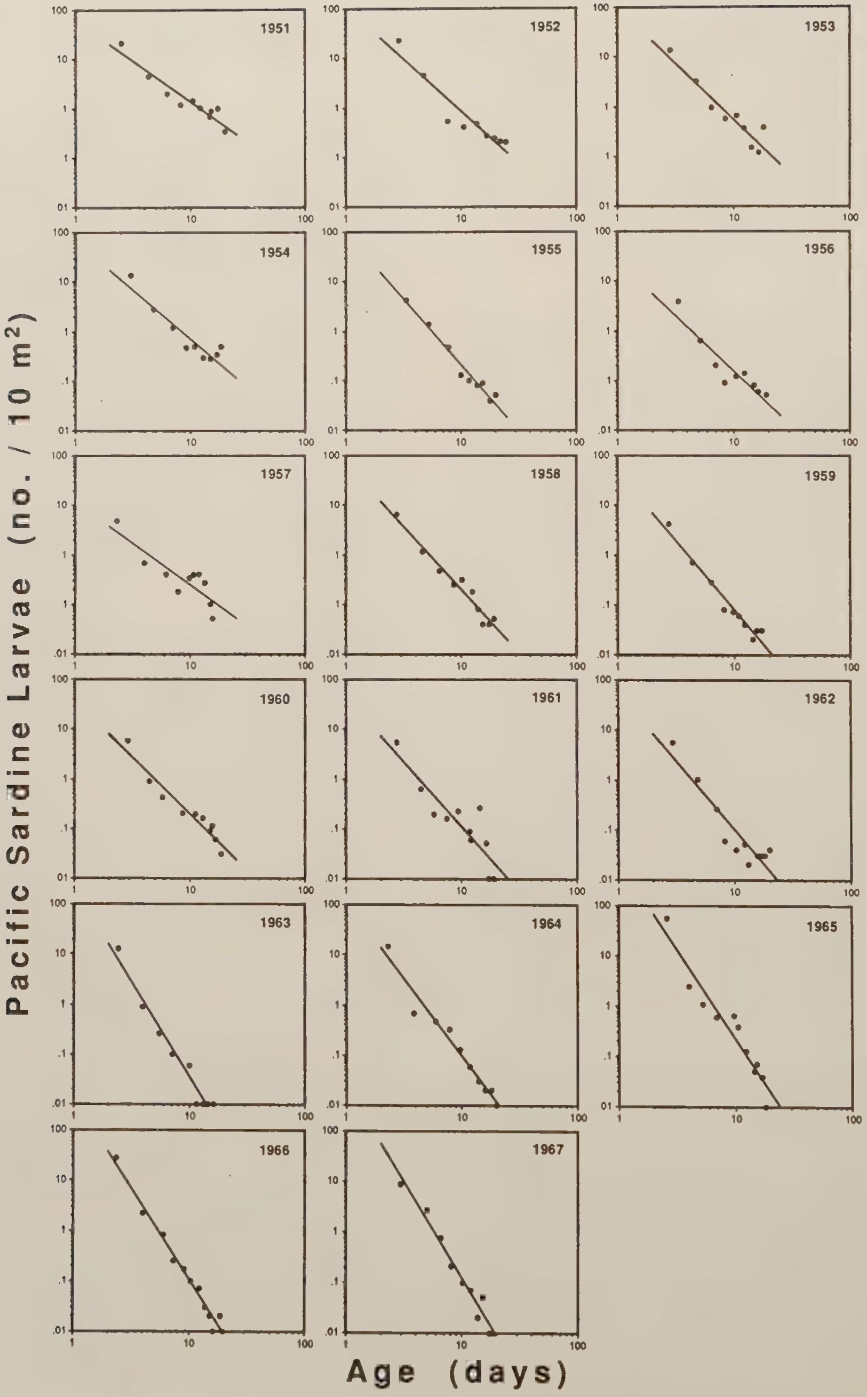

FIG. 2. Abundance of Pacific sardine larvae as a function of age for 1951–67.

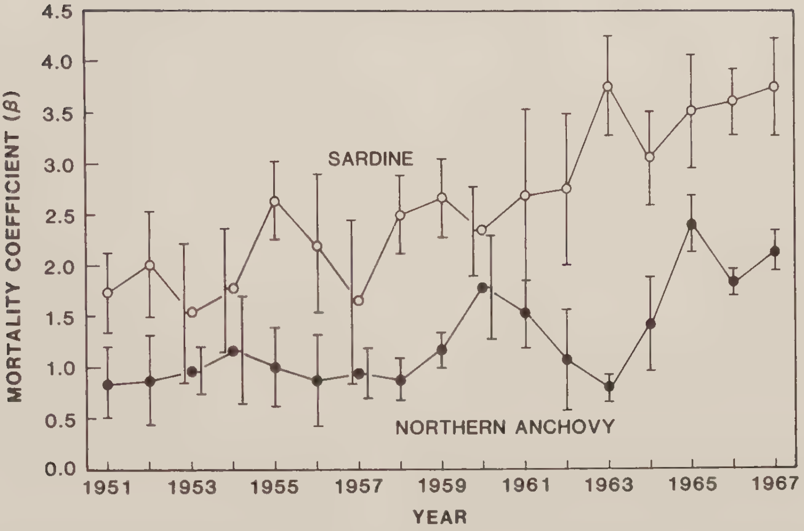

FIG. 3. Increase in the larval mortality coefficient, β, during 1951–67 for Pacific sardine and northern anchovy.

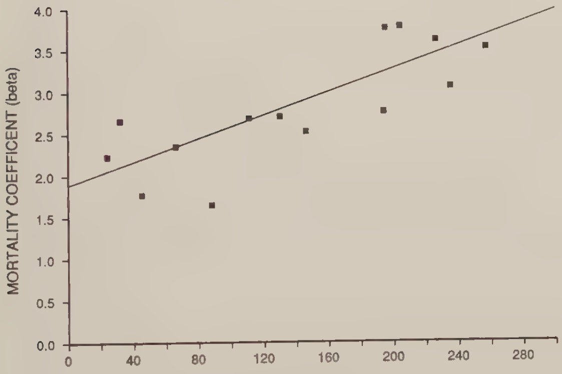

FIG. 4. Correlation of interannual variation of the larval mortality coefficient, β, of Pacific sardine and total biomass of northern anchovy.

other factor which affects mortality and recruitment. To test for an alternative explanation, I performed correlation analyses with some of the other factors which might be operating. These were temperature, geographic locality, small plankton abundance, salinity, turbulent mixing, and offshore transport.

Because larval sardine growth rates are correlated with temperature (Castillo et al. 1986) and growth rates determine the duration of larvae in each length class, temperature may affect mortality in an important way. Temperature is also used to calculate embryonic growth rates, which are then used to calculate mortality rates ($dN/dt = dN/dL \cdot dL/dt$ where dL is a length interval); a positive correlation with mortality rates is expected if temperature is confounded with mortality rates. However, lower temperature may slow the rate of development and extend the time that larvae experience high mortality at small sizes. Thus, a negative relationship between mortality and temperature is also conceivable. At stations yielding sardine larvae, temperatures ranged from 10.7 to 27.4°C. The annual weighted means ranged only from 15.6 to 23.2°C (Table 4). These temperatures were not significantly correlated with larval sardine mortality rate ($R^2 = 0.172$, $N^* = 15$, $P > 0.10$). Thus, I reject temperature as an important factor contributing to larval mortality.

To investigate whether there were significant interactions between mortality rates and any other variable, I tested the relationship using stepwise multiple correlation with temperature, latitude, small plankton volume, and Scripps Pier salinity anomalies, an index of turbulent mixing derived from wind data, an index of offshore transport, and the biomass of sardine, the biomass of anchovy, and the biomass of Pacific mackerel. The only significant correlation detected was between larval sardine mortality rates and anchovy biomass, and this correlation was positive. The coefficient of determination of β and anchovy biomass was 0.63 ($N^* = 9, P = 0.001$). The multiple correlation of β and anchovy biomass and small zooplankton volumes as a second correlate was not significant ($R^2 = 0.74$, $N^* = 9$, $P = 0.07$). Thus, the abundance of anchovy is the most important variable tested that explains the interannual variability in larval sardine mortality rates.

Larval mortality rates are only one factor in the process of recruitment. Because sardines enter the fishery at age 2, considerable mortality must occur between the larval phase and recruitment. To test whether larval mortality rates are a predictive indicator of recruitment, I regressed them against biomass at age. The association was not significant, although the sign of the relationship was negative as expected.

To investigate whether recruitment declined due to density-dependent effects on larval mortality rates (β), I regressed the logarithm of ratio of recruits at age 2 and the spawning biomass lagged by 2 yr as an index of recruitment success on both sar-

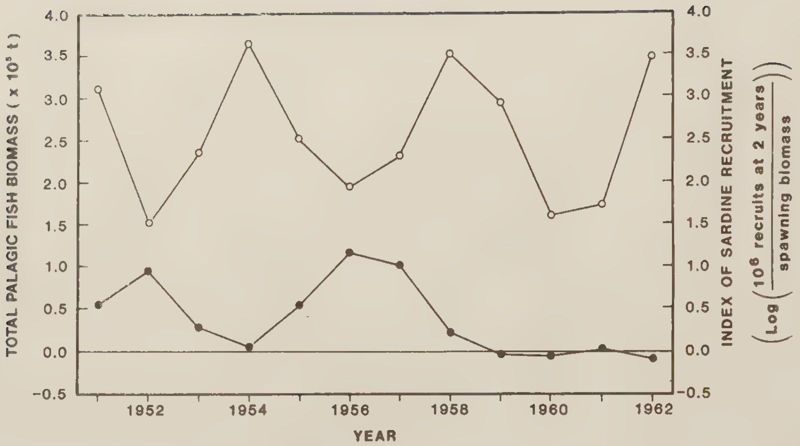

FIG. 5. Time series of total pelagic fish biomass (open circles) (Pacific sardine, northern anchovy, and Pacific mackerel) and recruitment index (solid circles) of Pacific sardine.

dine spawning biomass and β. Neither sardine biomass ($N^* = 11$, $P = 0.717$), nor β ($N^* = 10$, $P = 0.16$), nor the two variables in combination predicts recruitment success.

I also tested whether any other environmental factor was a reliable predictor of recruitment success: temperature, zooplankton volumes, latitude of center of spawning, sardine biomass, anchovy biomass, Pacific mackerel biomass, total pelagic fish biomass (anchovy, sardine, and Pacific mackerel), average sea level anomaly, and wind speed index. Again, total pelagic fish biomass ($N^* = 12$, $P = 0.03$) and anchovy biomass ($N^* = 9$, $P = 0.08$) were significantly negatively correlated with sardine recruitment success. Thus, no environmental factor, other than the abundance of predators, predicts sardine recruitment success.

Discussion

Larval Mortality

The mortality of Pacific sardine larvae was greater than that of northern anchovy larvae from 1951 to 1967 ($T = 9.09$, df = 16, $P << 0.01$). Others have reported similar results. Smith (1973, 1985) found that the ratio of the abundance of Pacific sardine larvae to sardine eggs in ichthyoplankton net tows was less than the corresponding ratio in northern anchovy, indicating that the mortality rates of larval sardines are indeed higher than those of larval anchovy. Smith et al. (1989) found higher mortality in sardine eggs than in Peruvian anchovy eggs in the same water mass.

Analysis of swimming energetics (Webb and Weihs 1986) and distribution of prey items (Vlymen 1977) also suggest greater mortality rates for faster growing larvae. Faster growing larvae must search greater volumes of water to obtain more food, and in so doing are at greater risk to predation than slower growers. On the other hand, lesser mortality rates for faster growing fish larvae are suggested by the relationship of particle size and mortality (Brooks 1968; Peterson and Wroblewski 1984; Kirkpatrick 1984), i.e. mortality in the sea is inversely related to body size. Faster growing fish larvae are subject to high mortality rates associated with small size but for a shorter period of time than slow-growing larvae. Because the mortality of the faster growing sardine larvae is greater than the mortality of the slower growing anchovy larvae, the energetic arguments of Webb and Weihs (1986) and Vlymen (1977) are supported by this analysis.

Behavioral differences observed in the laboratory may explain the observed differences in mortality rates. At a given age, fewer sardine larvae than anchovy larvae escape attack by adult anchovy (Butler and Pickett 1987). If predation contributes a significant fraction of larval mortality, then the greater vulnerability to visual predators of sardine larvae would contribute to a greater mortality rate. The observation by Brownell (1985) that Cape anchovy, *Engraulis capensis,* cannibalize larvae and juveniles as large as 50% of their own length supports the idea that anchovy may contribute to sardine mortality at lengths longer than the 20 mm considered here.

Stable Ocean Hypothesis

The lack of correlation between the number of calm days at 27°N, 116°W and larval sardine mortality rates does not support the hypothesis that periods of calm weather are necessary for the survival of all larval fish. This lack of correlation may be due in part to the absence of a strong signal in wind speed at this location. In the California Current regions, most of the strong wind events are related to storms which originate in the North Pacific. These storms reach southern California only infrequently, and their effects are less in northern Baja California.

In order for mixing to have an impact on larval mortality rates or recruitment, it must affect a significant portion of the population. Because most sardine spawning was well to the south of Point Conception, it is unlikely that storms and the resulting instability of the water column play a major role affecting the survival of sardine larvae in the California Current. Thus, Peterman and Bradford's (1987) conclusion that Lasker's stable ocean hypothesis accounts for a significant fraction of the interannual variability in the mortality of anchovy larvae is not extended to sardine larvae by this analysis.

The stable ocean hypothesis may explain the mortality of first-feeding anchovy larvae, but it does not explain recruitment

(Peterman et al. 1988). Evidence that starvation is not an important factor after the first-feeding stage has been presented by Owen et al. (1990) who found no difference in starvation rates, growth rates, or mortality rates of anchovy larvae in two areas of the California Current characterized by contrasting biomasses of plankton as collected by 45-μm-mesh nets. Lack of variation of larval anchovy growth rates between El Niño and non-El Niño years also casts doubt on the starvation hypothesis (Butler 1989).

Transport Hypothesis

Hjort's (1913) hypothesis that year class strength was determined early in life of fishes and that the sources of mortality of larval fish were due to starvation of first-feeding larvae or to transport out of feeding grounds has been the basis of much fisheries research. Based on the analysis of larval mortality rates and transport both southerly and offshore, there is no support for either component as a mechanism determining sardine larval mortality rates. Nor is there support for the hypothesis that offshore transport affects recruitment success to the adult population.

Whether southerly transport affects recruitment is debatable. The sea level anomaly, as an index of transport, has been correlated with recruitment to the Pacific mackerel population (Sinclair et al. 1985). Recruitment of 2-yr-old sardines is also correlated with the sea level anomaly (MacCall 1979 and above). This correlation may be due to the increased availability of 2-yr-old sardines off Southern California during the El Niño years of 1957–58 (MacCall 1979). If the El Niño years are excluded from the analysis, there is no correlation. However, eliminating El Niño years might exclude the conditions which would produce the hypothesized effect.

Examination of the aged landings (MacCall 1979, table 1) suggests that either the 1957 and 1958 year-classes were overrepresented or those year-classes incurred greater than normal mortality in the ensuing years. Furthermore, if the sea level anomaly is compared with recruitment, using a 2-yr time lag to test the effect of southerly transport during the year that the eggs were spawned, then the correlation is negative, but not significant. Thus, Hjort's (1913) second hypothesis that transport away from nursery grounds is not strongly supported by this analysis.

Predation Hypothesis

Although the predation hypothesis is supported by the evidence presented here, none of the other hypotheses can be categorically rejected. However, no correlation other than with predators could explain the observed trend in larval mortality rates. Predation is also consistent with the observed trend in recruitment.

Cannibalism of eggs and larvae in anchovies is well known (de Ciechomski 1967; Hayasi 1967; Loukashkin 1970; Hunter and Kimbrell 1980; MacCall 1980; Santander et al. 1983; Alheit 1987; Smith et al. 1989). In the northern anchovy, cannibalism can account for 20–28% of the observed egg mortality (Hunter and Kimbrell 1980). In an analysis of cannibalism by the Peruvian anchoveta, Alheit (1987) found that cannibalism accounted for 22% of the egg mortality. Stomachs of Pacific sardine in the same area also contained anchoveta eggs. On a per-weight basis, Alheit (1987) estimated that sardines may consume as many as or more anchoveta eggs than the anchoveta. Together, the two species may account for about 50% of the daily anchoveta egg mortality.

If northern anchovy filter their own eggs, then they must certainly also feed on other fish eggs and larvae. Perhaps because of the thin integument of larval fish and because of rapid digestion rates, fish larvae are rarely found in the stomachs of anchovy (Hunter and Kimbrell 1980). Fish eggs reported in the stomachs of anchovy by Loukashkin (1970) were not identified. Northern anchovy occurs with sardine during spawning (Ahlstrom 1967) and thus could consume significant numbers of eggs and larvae. Cannibalism is also consistent with the observed trend in anchovy larval mortality rates, but this effect was discounted by Peterman and Bradford (1987) due to the confounding of the slope (mortality) and the intercept (spawning biomass) of larval production and because mortality was more strongly correlated with water column stability. However, Pepin (1987) extended the analysis to predator to prey ratios and found that anchovy larval mortality rates were related to predation by total pelagic fish biomass.

Smith (1985) listed three situations in which cannibalism by schooling pelagic fishes would be effective in population control: (1) directed filtering behavior on dense aggregations of eggs, (2) encounter with other schools' patches of eggs, and (3) anchovy population switching from biting to filtering behavior. The correlation of mortality rates with predator to prey ratios is support for the later scenario. The same three situations also apply to predation of schooling pelagic fish on the eggs and larvae of other fishes, and the latter two scenarios are consistent with the observed trends in Pacific sardine larval mortality and northern anchovy biomass.

Conclusions

Competition between adults (Murphy 1966) or between larvae (Marr 1960) has been suggested as the important interactions between sardine and anchovy. Between 1951 and 1967, it is unlikely that the abundance of either species or their total biomass could have affected their food supply significantly. The biomass of sardines is far below its maximum in the 1930's. It is also unlikely that the biomass of fish larvae ever affects larval food densities (Cushing 1983). But Jones (1989) argued that larval fish may consume a significant fraction of secondary production and that resource limitation is possible for larval fish. Owen et al. (1990) found no difference in larval growth rates between sites with contrasting microzooplankton densities. The correlation of larval sardine mortality with anchovy abundance indicates an important interaction between the two species which has not been documented previously.

The decline of the Pacific sardine fishery during the late 1940's and 1950's has been ascribed to overfishing during periods of poor recruitment (Clark, in Clark and Marr 1955; Murphy 1966; MacCall 1979). Marr (1960) found no obvious relationship between parent stock size and recruitment and concluded that environmental change was responsible for recruitment failure and the decline of the Pacific sardine stock. Iles (1973) also suggested climatic change as the agency of recruitment failure of the Pacific sardine.

Analyzing the waning years of the sardine fishery, MacCall (1979) noted a "string of poor recruitments since 1958. . .remarkable in its duration and magnitude." The increase in larval mortality rates during the time period is also remarkable for its duration and magnitude. The correlation of the larval mortality rates with anchovy biomass indirectly suggests that the two species interact by predation. Anchovy predation on eggs and young larvae (<20 d) would produce the observed correlation between anchovy biomass and larval sardine mortality rates. Predation on older larvae (>20 d) and young juveniles would explain the negative correlation between sardine recruitment and the combined biomass of pelagic fishes and would largely explain the string of poor recruitments observed in the 1960's.

Of the three hypotheses advanced to predict larval mortality rates, water column stability and starvation of larvae, transport away from nursery grounds, and predation, only predation explains the observed trends in larval sardine mortality rates and recruitment success.

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References

Ahlstrom, E. H. 1967. Co-occurrence of sardine and anchovy larvae in the California current region off California and Baja California. Calif. Coop. Oceanic Fish. Invest. Rep. 11: 117–135.

Alheit, J. 1987. Cannibalism versus egg predation: their significance in anchovies, p. 467–470. *In* A. I. L. Payne, J. A. Gulland, and K. H. Brink [ed.]. The Benguela and comparable ecosystems. Afr. J. Mar. Sci. 5.

Bakun, A. 1973. Coastal upwelling indices, West Coast of North America, 1946–71. NOAA Tech. Rep. NMFS SSRF-671: 103 p.

1985. Comparative studies and the recruitment problem: searching for generalizations. CalCOFI Rep. XXVI: 30–40.

Bayley, G. V., and J. M. Hammersley. 1946. The effective number of independent observations in an autocorrelated series. J. R. Stat. Soc. Ser. B 8: 184–197.

Bissell, A. F. 1972. A negative binomial model with varying element sizes. Biometrika 59: 435–441.

Blackman, R. B., and J. W. Tukey. 1958. The measurement of power spectrum from the point of view of communications engineering. Dover Publishing, Inc., New York, NY. 190 p.

Brewer, G. D., G. S. Keppel, and M. Dempsey. 1984. Apparent predation on ichthyoplankton by zooplankton and fishes in nearshore waters of southern California. Mar. Biol. 80: 17–28.

Brooks, J. L. 1968. The effects of prey size selection by lake planktivores. Syst. Zool. 17: 272–291.

Brownell, C. L. 1985. Laboratory analysis of cannibalism by larvae of the Cape anchovy *Engraulis capensis*. Trans. Am. Fish. Soc. 114: 512–518.

Butler, J. L. 1987. Comparison of the early life history parameters of Pacific sardine and northern anchovy and implications for species interactions. Ph.D. thesis, University of California at San Diego, San Diego, CA. 242 p.

1989. Growth during the larval and juvenile stages of the northern anchovy, *Engraulis mordax*, in the California Current during 1980–84. Fish. Bull. U.S. 87: 845–852.

Butler, J. L., and B. R. de Mendiola. 1985. Growth of larval sardines off Peru. CalCOFI Rep. XXVi: 113–118.

Butler, J. L., and D. Pickett. 1987. Age-specific vulnerability of sardine larvae to predation by northern anchovy. Fish. Bull. U.S. 86: 163–168.

Castillo, G., E. Aquilera, G. Herrera, P. A. Bernal, J. Butler, J. Chong, H. Gonzalez, C. Oyarzun, and C. Veloso. 1986. Larval growth rates of the Pacific sardine *Sardinops sagax* off central Chile, determined by daily ring counts in otoliths. Biol. Pesq. 14: 3–10.

Chelton, D. B. 1980. Low frequency sea-level variability along the west coast of North America. Ph.D. thesis, University of California at San Diego, San Diego, CA. 212 p.

Chelton, D. B., P. A. Bernal, and J. A. McGowan. 1982. Large-scale interannual physical and biological interaction in the California Current. J. Mar. Res. 40: 1095–1125.

Clark, F. N., and J. C. Marr. 1955. Population dynamics of the Pacific sardine. Prog. Rep. Calif. Coop. Ocean. Fish. Invest. 1953–1955: 11–48.

Cushing, D. H. 1983. Are fish larvae too dilute to affect the density of their food organisms J. Plankton Res. 5: 847–854.

de Ciechomski, J. 1967. Investigations of food and feeding habits of larvae and juveniles of the Argentine anchovy *Engraulis anchoita*. Calif. Coop. Oceanic Fish. Invest. Rep. 11: 72–81.

Frank, K. T., and W. C. Leggett. 1984. Selective exploitation of capelin (*Mallotus villosus*) eggs by winter flounder (*Pseudopleuronectes americanus*): capelin egg mortality rates, and contribution of egg energy to the annual growth of flounder. Can. J. Fish. Aquat. Sci. 41: 1294–1304.

Hayasi, S. 1967. A note on the biology and fishery of the Japanese anchovy, *Engraulis japonica* (Houttuyn). Calif. Coop. Oceanic Fish. Invest. Rep. 11: 44–57.

Hewitt, R. P., G. H. Theilacker, and N. C. H. Lo. 1985. Causes of mortality in young jack mackerel. Mar. Ecol. Ser. 26: 1–10.

Hjort, J. 1913. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 20: 1–228.

1926. Fluctuations in the yearclasses of important food fishes. J. Cons. Int. Explor. Mer 1: 5–38.

Hunter, J. R. 1984. Inferences regarding predation on the early life history stages of cod and other fishes. Flodevigen rapportser. 1. ISSN 0333—2594. The propagation of cod *Gadus morhua*. p. 533–562.

Hunter, J. R., and C. A. Kimbrell. 1980. Egg cannibalism in the northern anchovy, *Engraulis mordax*. Fish. Bull. U.S. 78: 811–816.

Iles, T. D. 1973. Interaction of environment and parent stock size in determining recruitment in the Pacific sardine as revealed by analysis of density-dependent 0-group growth. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 164: 228–240.

Jones, R. 1989. Towards a general theory of population regulations in marine teleosts. J. Cons. Int. Explor. Mer 45: 176–189.

Kirkpatrick, M. 1984. Demographic models based on size, not age, for organisms with indeterminate growth. Ecology 65: 1864–1884.

Kramer, D., M. J. Kalin, E. G. Stevens, J. R. Thrailkill, and J. R. Zweifel. 1972. Collecting and processing data on fish eggs and larvae in the California Current region. NOAA Tech. Rep. NMFS Circ-370: 38 p.

Laird, A. K. 1967. Evolution of the human growth curve. Growth 32: 347–354.

Lasker, R. 1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull. U.S. 73: 453–462.

1978. The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. Rapp. P.-V. Réun. Cons. Int. Explor. Mer. 173: 212–230.

1981. The role of a stable ocean in larval fish survival and subsequent recruitment, p. 80–88. *In* R. Lasker [ed.] Marine fish larvae: morphology, ecology and relation to fisheries. Washington Sea Grant, Seattle, WA.

Lenarz, W. H. 1972. Mesh retention of larvae of *Sardinops caeruleus* and *Engraulis mordax* by plankton nets. Fish. Bull. U.S. 70: 839–848.

1973. Dependence of catch rates on size of fish larvae. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 164: 270–275.

Lillelund, K., and R. Lasker. 1971. Laboratory studies of predation by marine copepods on fish larvae. Fish. Bull. U.S. 69: 655–667.

Lo, N. C. H. 1983. Re-estimation of three parameters associated with anchovy egg and larval abundance: temperature dependent incubation time, yolk-sac growth rate and egg and larval retention in mesh nets. U.S. Dep. Commer. NOAA Tech. Memo. SWFC-TM-NMFS-31: 32 p.

1985. Egg production of the central stock of northern anchovy, *Engraulis mordax*, 1951–82. Fish. Bull. U.S. 83: 137–150.

Loukashkin, A. S. 1970. On the diet and feeding behavior of the northern anchovy, *Engraulis mordax* (Girard). Proc. Calif. Acad. Sci. Ser. 4 37: 419–458.

MacCall, A. E. 1979. Population estimates for the waning years of the Pacific sardine fishery. Calif. Coop. Oceanic Fish. Invest. Rep. 20: 72–82.

1980. The consequences of cannibalism in the stock–recruitment relationship of planktivorous pelagic fishes such as *Engraulis*, p. 201–220. *In* G. D. Sharp [ed.] Workshop on the effects of environmental variation on the survival of larval fishes. Intergovernmental Oceanographic Commission, IOC/UNESCO Paris, Workshop Report 28.

Marr, J. C. 1960. The causes of major variations in the catch of Pacific sardine *Sardinops caerulea* (Girard), p. 667–791. *In* Proceedings of the World Scientific Meeting on the Biology of Sardines and Related Species, FAO, UN, Rome, Italy. Vol. 3.

Methot, R. D. 1986. Synthetic estimates of historical abundance and mortality for the northern anchovy, *Engraulis mordax*. NOAA-NMFS-SWFC Admin. Rep. LJ 86 –29: 42 p.

Möller, H. 1984. The reduction of a larval herring population by jellyfish predator. Science (Wash., DC) 224: 621–622.

Murphy, G. I. 1966. Population biology of the Pacific sardine (*Sardinops caerulea*). Proc. Calif. Acad. Sci. 34: 1–34.

O'Connell, C. P. 1980. Percentage of starving northern anchovy estimated by histological methods. Fish. Bull. U.S. 78: 475– 484.

Owen, R. W., N.C. H. Lo, J. L. Butler, G. H. Theilacker, A. Alvarino, J. R. Hunter, and Y. Watenabe. 1990. Spawning and survival patterns of larval northern anchovy, *Engraulis mordax*, in contrasting environments — a site-intensive study. Fish. Bull. U.S. 87: 673–688.

Parrish, R., and A. E. MacCall. 1978. Climatic change and exploitation in the Pacific mackerel fishery. Calif. Dep. Fish Game Fish Bull. 167: 1–109.

Parrish, R., C. S. Nelson, and A. Bakun. 1981. Transport mechanisms and reproductive success of fishes in the California Current. Biol. Oceanogr. 1: 175–203.

Pepin, P. 1987. Influence of alternative prey abundance on pelagic fish predation of larval fish: a model. Can. J. Fish. Aquat. Sci. 44: 222–227.

Peterman, R. M., and M. J. Bradford. 1987. Wind speed index correlates with mortality rate of a marine fish, the northern anchovy (*Engraulis mordax*). Science (Wash., DC) 235: 354 –366.

Peterman, R. M., M. J. Bradford, N. C. H. Lo, and R. D. Methot. 1988. Contribution of early life stages to interannual variability in recruitment of northern anchovy (*Engraulis mordax*). Can. J. Fish. Aquat. Sci. 45: 8–16.

Peterson, I., and J. S. Wroblewski. 1984. Mortality rate of fishes in the pelagic ecosystem. Can. J. Fish. Aquat. Sci. 41: 1117–1120.

Purcell, J. E. 1985. Predation on fish eggs and larvae by pelagic cnidarians and ctenophores. Bull. Mar. Sci. 37: 739–755.

Purcell, J. E., T. D. Siferd, and J. B. Marliave. 1987. Vulnerability of larval herring to capture by the jellyfish, *Aequorea victoria*. Mar. Biol. 94: 157–162.

Santander, H., J. Alheit, A. D. MacCall, and A. Alamo. 1983. Egg mortality of the Peruvian anchovy (*Engraulis ringens*) caused by cannibalism and predation by sardines (*Sardinops sagax*). FAO Fish. Rep. 291: 1011–1025.

Simpson, J. J., and T. D. Dickey. 1981. The relationship between downward irradiance and upper ocean structure. J. Phys. Oceanogr. 11: 309–323.

Sinclair, M., M. J. Tremblay, and P. Bernal. 1985. El Niño events and variability in a Pacific mackerel (*Scomber japonicus*) survival index: support for Hjort's second hypothesis. Can. J. Fish. Aquat. Sci. 42: 602–608.

Smith, P. E. 1973. The mortality and dispersal of sardine eggs and larvae. Rapp. P.-V. Réun. Cons. Int. Exp. Mer 164: 282–292.

1985. A case history of an anti-El Niño to El Niño transition on plankton and nekton distribution and abundances, p. 121–142. *In* W. S. Wooster and D. L. Fluharty [ed.] El Niño North, Niño effects in the Eastern Subarctic Pacific Ocean. Washington Sea Grant, Seattle, WA.

Smith, P. E., H. Santander, and J. Ahlheit. 1989. Comparison of the mortality rates of Pacific sardine, *Sardinops sagax*, and Peruvian anchovy, *Engraulis ringens*, eggs off Peru. Fish. Bull. U.S. 87: 497–508.

Sutcliffe, W. H. Jr., R. H. Loucks, and K. F. Drinkwater. 1976. Coastal circulation and physical oceanography of the Scotian Shelf and the Gulf of Maine. J. Fish. Res. Board Can. 33: 98–115.

Theilacker, G. H. 1986. Starvation-induced mortality of young sea-caught jack mackerel, *Trachurus symmetricus*, determined with histological and morphological methods. Fish. Bull. U.S. 84: 1–15.

Theilacker, G. H., and R. Lasker. 1974. Laboratory studies of predation by euphausid shrimps on fish larvae, p. 287–299. *In* J. H. S. Blaxter [ed.] The early life history of fish. Springer Verlag, Berlin.

Van der Veer, V. W. 1985. Impact of coelenterate predation on larval place Pleuronectes platessa, and flounder *Platichthys flesus* in the western Wadden Sea. Mar. Ecol. Prog. Ser. 25: 229–238.

Vlymen, W. J. 1977. A mathematical model of the relationship between larval anchovy (*Engraulis mordax*) growth, prey microdistribution, and larval behavior. Environ. Biol. Fishes 2: 211–233.

Walford, L. A. 1946. Correlation between fluctuations in abundance of the Pacific sardine (*Sardinops caerulea*) and salinity of sea water. J. Mar. Res. 6: 48–53.

Webb, P. W., and D. Weihs. 1986. Functional locomotor morphology of early life history stages of fishes. Trans. Am. Fish. Soc. 115: 115–127.

Zweifel, J. R., and R. Lasker. 1976. Prehatch and posthatch growth of fishes — a general model. Fish. Bull. U.S. 74: 609–621.

Zweifel, J. R., and P. E. Smith. 1981. Estimates of abundance and mortality of larval anchovies (1951–75): application of a new method. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 178: 248–259.

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Application of Line Transect Methods to Surveying Demersal Communities with ROVs and Manned Submersibles

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ABSTRACT

The traditional method of estimating the abundance of demersal fishes is the swept-area trawl method. This method has many biases and is limited to smooth bottom. The Southwest Fisheries Science Center is developing innovative stock assessment methodology to improve population estimates of important fishery resources in the U. S. Exclusive Economic Zone (EEZ). Manned submersibles or ROVs, equipped with both still and video cameras will be used to record images along sea-floor transects. This method will allow for sampling of areas unavailable to traditional methods (e.g. rocky substrate). Line transect estimates from the survey vehicle will be compared to traditional trawl estimates on trawlable substrate. Density estimates obtained from samples stratified by depth and bottom roughness will be used to make population estimates using stratum areas quantified by multibeam surveys. Integrating habitat specific estimates of fisheries resources with multibeam data will provide a new application for existing NOAA multibeam sonar data, as well as previously unattainable precision in fishery assessment. Survey data will provide in situ evidence of habitat use by fishery resources. The analysis of trawl tracks will document the effect of man's activities (trawling) on this habitat.

INTRODUCTION

Management of demersal fish species is based on a combination of fishery dependent data obtained from catch sampling to provide information on the relative change in population size, and fishery independent data obtained from surveys to provide information on the absolute population size. Fish from catch sampling are aged and this age-structured information can be analyzed through cohort [1] or stock synthesis [2] analysis to give an accurate picture of how population size changes from one year to the next. Unfortunately it cannot give an indication of how close the actual population is to a threshold value of overfishing. Therefore absolute population estimates from fishery independent data are needed to anchor the relative trend obtained from the fishery dependent data.

Currently trawl surveys using nets similar to those used in the commercial fishery are the primary source of fishery independent data used in demersal fish management but these surveys have several serious problems. The most serious problem is that the mean values from trawl surveys have very large variances which tend to be related to the mean, with means and variances both increasing together rather than being independent [3]. This results in confidence intervals around means that range from 50 to 100% for flatfish species and that are greater than 100% for rockfish species, *Sebastes* spp. [4]. As a result, all but the most severe changes in population size are masked by these large confidence intervals. Methods that have been commonly used to deal with this variability are transformations using either the negative binomial [3] or the delta [5] distribution. Data transformed using these distributions more closely follow the observed mean to variance relationship, however the large confidence intervals and variances remain. Other problems with trawl survey data are uncertainties due to fish behavior (avoidance and off-bottom migration), the area swept by the trawl and fish escapement through the net.

Here we describe two new methods of making absolute population estimates from fishery independent data, observer transects and video transects. The observer transects are made from manned submersibles and the video transects are made from both manned submersibles and remotely operated manned vehicles (ROV). The advantages and disadvantages of both transect types are specified and compared to the currently used trawl surveys.

METHODS

Sampling Design

Isobath The traditional method of sampling demersal fishes has been with trawl samples taken at discrete depths. Samples have been taken systematically with depth (every 100 m) or stratified randomly with depth. In reality the samples are not taken along the isobath. The course of the ship while the trawl is on the bottom is determined by the direction of the wind and the seas. Unless the bottom is very flat or the isobaths are parallel to the direction of the seas, the trawl will sample across the isobaths.

Transects along isobaths replicate trawling and maximize information about within strata heterogeneity. This approach has two disadvantages. If distributions of species are strongly determined by depth and the transect happens to fall on a boundary, the sample may be highly biased. From a practical standpoint it is very difficult to maneuver a manned submersible or ROV along the isobath. This is especially true along steep terrain when the pilot cannot see the bottom. The amount of time actually viewing the substrate is reduced when the vehicle maneuvers across steep ravines.

Gradient Making transects up slope has the advantage of crossing important gradients (depth, light, oxygen) on each dive. Each observation provides information on distribution and abundance of organisms with respect to depth[6]. For that reason it is critical to record depth constantly in order to facilitate later analysis. Abundance data may be post-stratified by depth to address questions concerning abundance within a given depth range.

A second advantage is efficient use of dive time. Since the pilot can see the substrate at all times, the effective survey time is maximized. Because the preferred orientation of the vehicle (both ROV and manned submersible) is tilted upward the amount of time in visual contact with the substrate is maximized. Surveying up slope also makes use of time that would be allocated to returning to the surface from a horizontal transit.

Configuration of Vehicles

It is beyond the scope of this paper to provide a comprehensive discussion of all of the manned submersible and ROV designs and accessory equipment available. The following section summarizes some attributes of manned submersibles and ROVs that pertain to their use in fisheries oceanography.

Manned submersible The configuration of manned submersibles is quite variable, but typically the pilot and observer(s) occupy a pressure hull along with a large quantity of equipment including life support systems. This compartment is contained within a larger structural frame that supports the batteries, flotation, variable ballast system, etc. Manned submersibles typically have two means for directly viewing the ocean outside the pressure hull, small circular view ports (11 cm diameter; e.g. Alvin, Pisces, Turtle) or an entire pressure hull manufactured from transparent material (Johnson Sea-link, Deep Rover). In manned submersibles with small view ports, the scientist/observer's view is normally very limited. For obvious reasons, the pilot's view is forward, and far superior to that of the scientist/observer. Both the pilot and observer have external lights that illuminate their fields of view. The acrylic view ports present a magnified image, confounding one's ability to estimate the size of objects in view. In manned submersibles with acrylic pressure hulls, the pilot and observer have a tremendous field of view. However, due to the shape of the pressure hull, the apparent size of objects is somewhat reduced.

ROV The configuration of ROVs for fishery research requires that every effort is made to collect and record the maximum amount of visual information. Details of these requirements will be discussed in various sections below. Briefly these requirements are high resolution video cameras, adequate lighting, and minimal loss of picture clarity in transmission. Only fiber optic tethers meet the last requirement. To survey fish at depths below about 400 m, a tether management system is necessary. The ROV must monitor and record information about altitude, camera angle, zoom and focus to provide data on the size of the field of view from the video camera. Laser spots, discussed below, provide a convenient way to spatially calibrate the video system.

Requirements for Video

Traditionally, video has been used to record movements and a continuous record of the dive's activities. Although video cameras and recorders serve this purpose well, their wider application has been limited by poor resolution and the difficulty of identifying organisms from tapes. With the increasing availability of high resolution cameras and recording media, video has become a viable alternative to still photographs for ecological studies.

Identification of organisms from visual cues is a difficult task. Standard taxonomic information (meristic characters such as dentition, number of gill rakers, fin ray counts, etc.) are not readily available. In addition, we have observed that live specimens do not look like dead or preserved specimens. Illustrations or pictures of dead fish in identification guides are often misleading. Thus, identification of live organisms from images requires experience and the greatest obtainable resolution in order to maximize the certainty of identification. For this reason and because of the power of continuous observation, high resolution video cameras and video recorders are the media of choice.

Camera There are a wide variety of video cameras and recording formats available; most of which have been utilized on manned submersibles and ROVs. Until very recently, the most commonly used video camera had resolutions of about 300 lines. In recent years, a number of higher resolution cameras and recording formats have become available at reasonable prices. Most video cameras today are based on solid state charge coupled devices (CCD). Cameras are available with one, two, and three CCDs. Single chip cameras are available with 400 lines of resolution. Two chip cameras with resolution of 500 lines are made specifically for the S-VHS recording format. Three chip cameras are made for broadcast quality applications and have resolutions up to 600 lines. These cameras output composite video, S-video or BetaCam component signals. With multiple chip cameras the light is split by prisms to 2 or 3 chips each of which has a different filter. Hence multiple chip cameras have much lower sensitivity than single chip cameras.

Recording formats are the limiting factor in video systems. No recording format equals the resolution of the highest resolution camera. The most common recording format in North America is VHS which has a resolution of 230 lines. S-VHS and Hi-8 recorders reproduce 400 lines of resolution. Both S-VHS and Hi-8 separate chromanance from luminance and record each on separate tracks to increase the signal to noise ratio. BetaCam reproduces 350 lines of resolution but the quality of the color image is far superior to S-VHS or Hi-8.

Lighting High resolution images require adequate lighting and color balance. Video cameras with three CCDs require more light than single chip cameras. Broadcast quality video cameras such as those based on the Sony DCX 3000 require 25 lux at F1.6. To obtain good color up to 2 meters from the camera, at least 3000 watts of light or 52,000 lumens is required[7]. Since red wavelengths are absorbed strongly in sea water, the light should be biased toward those wavelengths. Sodium scandium lamps produce light from 330 to 700 nm with the maximum in the orange wavelengths (590 nm)[8]. These lamps are ideally suited for color video. To reduce common volume scattering (backscatter), the lamps should be positioned away from the optical axis of the camera.

Lasers With the addition of lasers mounted parallel to the camera axis the size of organisms can be determined. Two lasers allow the scaling of organisms [9] and three lasers define the plane of view [10] with fixed focal length lenses. The addition of a fourth laser at an angle will provide this information for zoom lenses at any focal length. Using an image processing system and a real time frame grabber it will be possible to calibrate each video frame and to calculate the area covered by the transect (Daniel Davis,MBARI, pers. comm.).

Requirements for Still Photography

Camera Still cameras have been used extensively in the study of benthic biology to gather information on abundance and pattern in the distribution of megafauna [11,12] Megafauna are defined operationally as those animals, including fishes, large enough to be counted and identified in photographs of the sea floor [11,13]. A wide variety of still cameras with a variety of lenses have been used on manned submersibles and ROV's in both single and stereo modes. Stereo photographs can be used to measure distances within the field of view, and allow a tremendous amount of information to be gleaned from a single pair of photographs. However, stereo photogrammetry is not an efficient means for analyzing a large number of photographs where only a limited amount of information will be extracted from each frame (e.g. identity and counts of fish). A typical 35 mm sea camera consists of a chassis, film mechanism with electronic controller, and lens, all enclosed within a deep-sea pressure housing. The use of 70 mm film will result in a recording of more detail on the film at some costs to the user which include an increase in the size of the camera, and a decrease in the ease of processing. A common lens used in deep-sea cameras is a water-corrected 28 mm lens (Nikkor). For many applications, the widest angle lens is desirable, because it reduces the distance between the subject and the lens, thereby minimizing the loss of light due to attenuation and the loss of resolution due to particulate matter in the water.

Lighting and film Photographs of the sea floor at all but the shallowest depths are illuminated by strobe lights. Due to the severe absorption of light by water and to the scattering of light by particulate matter in the water, the amount of light required to illuminate a small area of sea floor is considerable. As is the case with video lighting, the quality of the light field that finally illuminates the image is dependent on many factors in addition to the output of the source. The type of reflectors and positioning of the strobe in relation to the camera are critical to optimal illumination. For example, illumination of particles in the water between the camera and object being photographed will greatly degrade the image. This problem has been termed common volume scattering. If the camera and strobe can be separated, this problem is minimized. The interplay between the amount of illumination and the speed of the film will determine the aperture at which photographs are taken. There are a number of new color, and black & white negative films (e.g. Fuji f-series motion picture film) that offer high speed alternatives to the more commonly used color transparency films (e-6 process).

Data logging To maximize the amount of information obtained from video surveys, all of the pertinent information must be recorded in the proper context. Depth, altitude, and position should be recorded at all times and be integrated with time or time codes on video tape.

Analysis of Still Photographs

Quadrat A common approach to estimating the abundance of animals is to count the number of individuals within a known size area or quadrat. This sampling technique is well suited to the analysis of the type of non-overlapping, still photographs, commonly obtained with towed camera systems [11,14]. Photographs obtained from ROVs and manned submersibles fall into two major categories; vertical and oblique. In vertical photographs, the axis of the camera is at a right angle to the sea floor, and distances and areas are uniform throughout the entire photograph. In oblique photographs the camera angle is inclined below the horizontal, and the scale within the photographs changes with distance from the camera (Figure 1). For this reason, oblique photographs may be more difficult to interpret quantitatively than vertical photographs. For example, the error in estimating the sizes of objects and areas increases quasi-exponentially with distance from the camera [15]. The scale within a photograph is typically determined by superimposing a grid of appropriate dimension. Grids are either drawn empirically from underwater photographs of scale markers on the sea floor or determined from photogrammetric principles as applied to deep-sea photographs. In the photogrammetric approach, a grid of the camera's field of view is determined from several critical variables: 1) the height of the camera off the sea floor, 2) the inclination of the camera's optical axis, and 3) the camera's angle of view (Figure 1). Specific details concerning assumptions and methods for constructing measuring grids for oblique photographs can be found in the literature [15,10].

In most photographic surveys of the sea floor, the probability of detecting an organism is not equal over the entire field of view. This can be the case for both vertical and oblique photographs although the problem is usually more pronounced in the latter. Visibility of animals on the sea floor depends on a variety of factors, including characteristics of the lighting (e.g. amount of backscatter), orientation of a given animal and its reflectivity, as well as the relief of the sea floor. To minimize bias due to difficulties in detecting animals within photographs, it has been suggested that the usable area within a photograph (= quadrat size) should be determined *a posteriori* [15,16].

Here we will briefly discuss this problem for the case of "forward-looking" oblique photographs, however this method can be applied in a radial fashion to vertical photographs. Data, collected as part of a larger study on slope-dwelling fishes off central California, will be used to illustrate detection functions for selected species of fish with potentially different appearances: *Sebastolobus* spp., a 10 to 80 cm scorpaenid fish, *Microstomus pacificus*, a 20 to 40 cm flatfish, and *Eptatretus* spp. a hagfish which was photographed both resting on the substrate and occupying burrows with only their snouts visible [17]. A computerized digitizing system was used to record the size and location of fish within a photograph [15,16]. The data were pooled from a series of still photographs taken with a towed camera sled.

Taxa-specific patterns in visibility were examined by an analysis of the probability of detection at increasing perpendicular distance from the camera sled's transect center line and longitudinal distance from the camera along the transect center line. In the case of perpendicular distance, the data were grouped into 13 intervals. The variation of probability density with perpendicular distance is shown in Figure 2 for all 4 fish taxa. Each bar in the histogram represents the probability of detection within a parallel "lane" on the sea floor, beginning 120 cm ahead of the camera sled (10x920 cm).

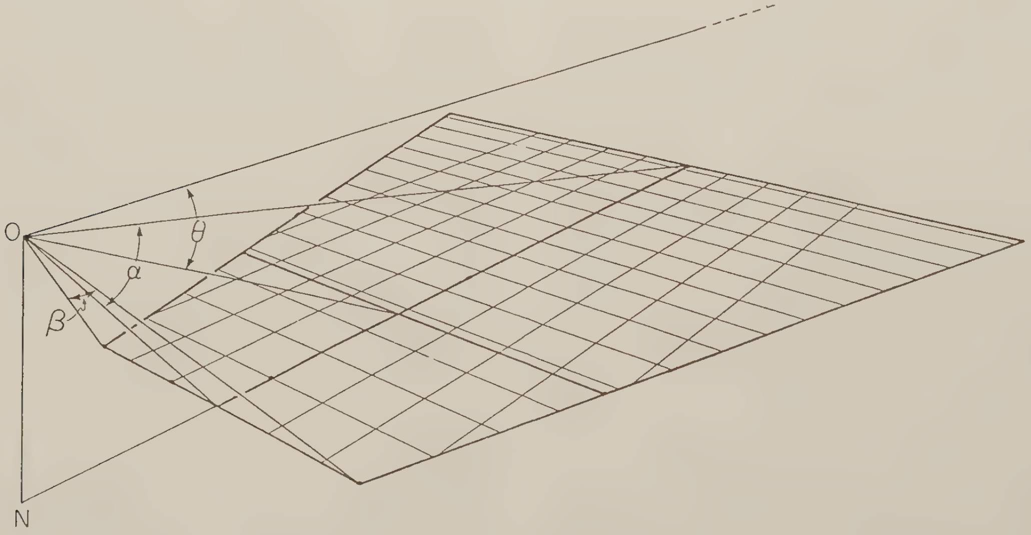

Figure 1. Representation of a perspective view of the sea floor where α and β correspond to the camera's horizontal and vertical angles of view, and θ is the inclination of the axis of the camera. The position of the camera lens is marked by O and the line o,n is the height of the camera above the substrate.

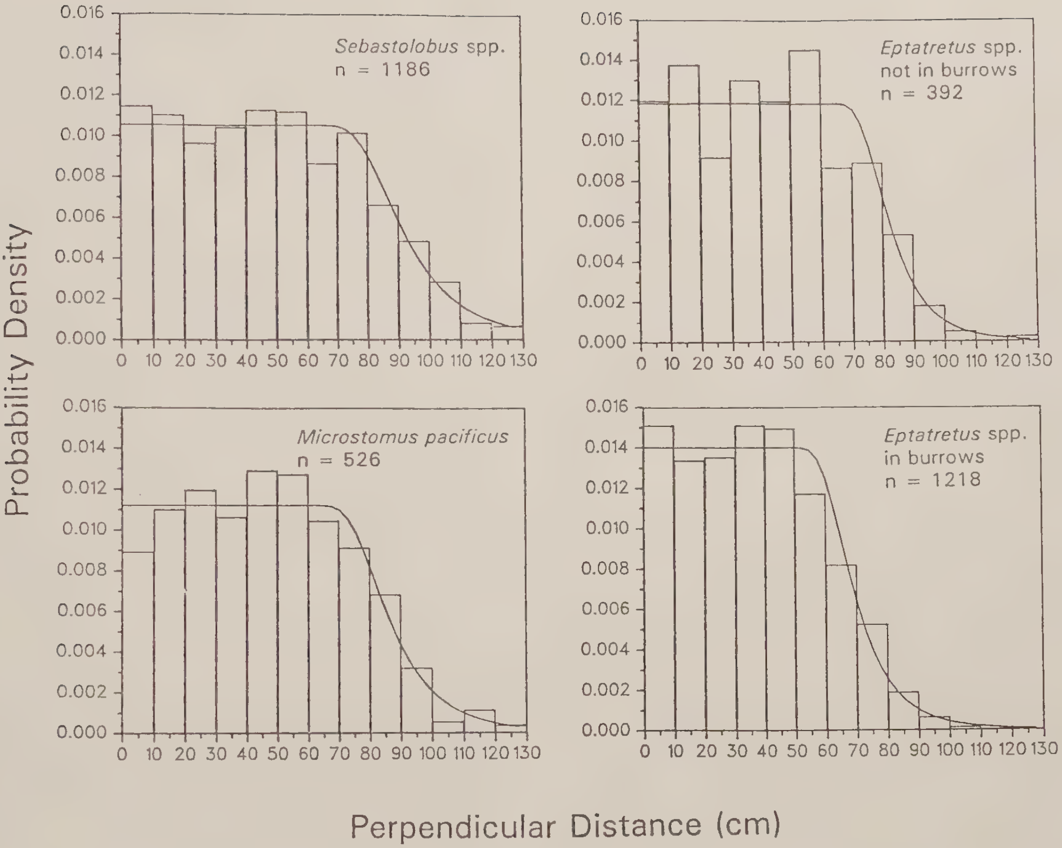

Figure 2. Observed probability of detection (bars) as a function of perpendicular distance (cm) from the trackline for 3 species of fish and hazard-rate model fitted to the data.

The line plotted over each histogram is the detection function for the hazard-rate model [18], and its importance will be discussed in the next section. Fish were visible out to a maximum perpendicular distance of 130 cm. Probability of detection was relatively constant out to a perpendicular distance of about 70 cm for *Sebastolobus*, *Microstomus*, and *Eptatretus* on the substrate after which it declined monotonically. For *Eptatretus* occupying burrows, a break in the probability of detection occurs at about 50 cm. These perpendicular distances define the usable "width" of quadrats for each species.

A similar approach can be used to define the taxa-specific limit for a quadrat in the direction moving out from the camera sled or in the "longitudinal direction". Probability of detection versus longitudinal distance (20 intervals) is plotted for the same four taxa of fish in Figure 3. Longitudinally, fishes were visible to distances in excess of 400 cm, but the longitudinal distance over which the probability of detection was constant varied between types of fish: 180 cm for *Sebastolobus* and *Microstomus*, 120 cm for *Eptatretus* on the substrate and 60 cm for *Eptatretus* in burrows. The extension of the usable area of sea floor along the transect center line varied by a factor of up to 3.

The perpendicular and longitudinal detection functions may be combined to derive the following taxa-specific quadrat sizes:

Fish Taxa	Quadrat Size (m^2)
Sebastolobus spp. thornyhead	2.5
Microstomus pacificus Dover sole	2.5
Eptatretus spp. hagfish on substrate	1.7
Eptatretus spp. hagfish in burrows	0.6

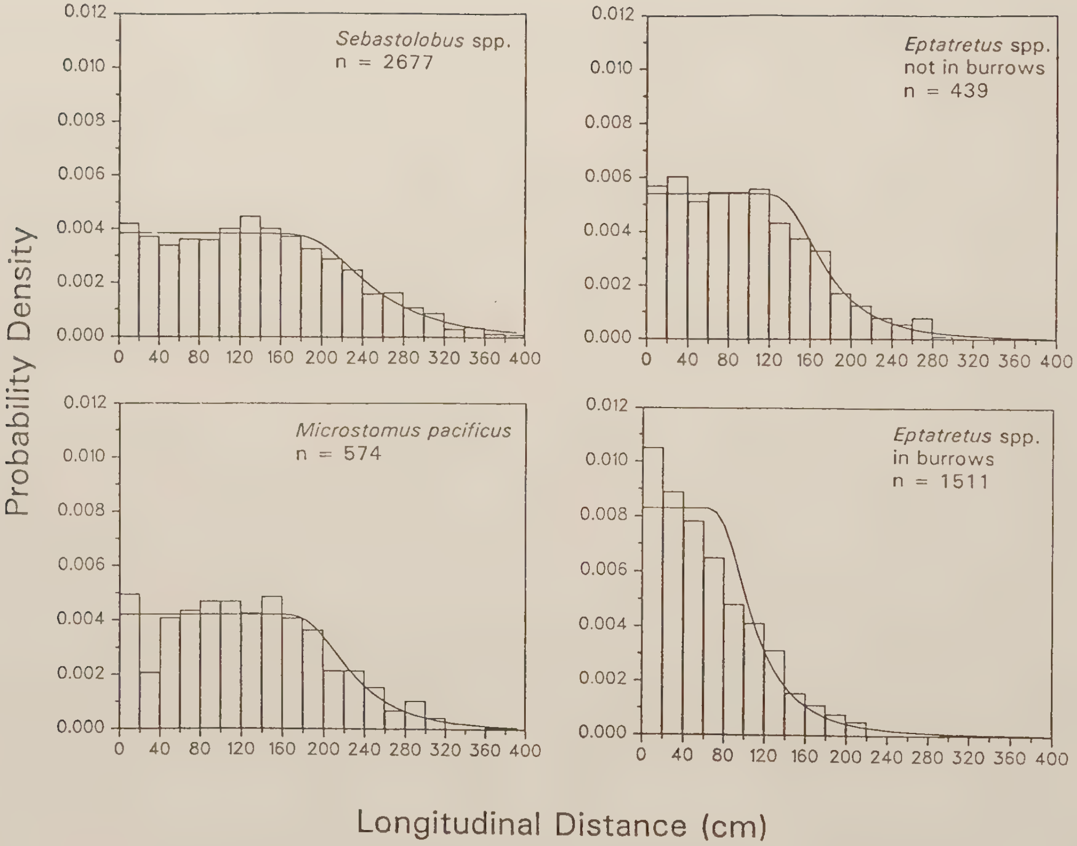

Figure 3. Observed probability of detection (bars) as a function of longitudinal distance (cm) from the trackline for 3 species of fish and hazard-rate model fitted to the data.

Analysis of Video

In the previous section, we demonstrated the use of quadrat sampling in the analysis of non-overlapping still photographs. In contrast, overlapping still photographs or continuous video footage taken along a transect center line require an alternative approach to sampling. Strip and line transect methods were developed to analyze data where an observer, or in our case, a camera, continuously records counts of animals along a transect center line or transect [19,20,21].

Strip transect In strip transect sampling, the probability of detecting a fish is assumed to be constant over some width (perpendicular distance) of the transect that was determined either before or after the survey. If we assume that detection functions derived from still photographs (Figure 2) approximate those for video footage, then there appears to be a strip within which the probability of detection is constant. However, as we have observed in the previous section, data collected beyond the point where the detection function declines is not included in the analysis. The choice of whether or not to use strip or line transect methods depends in part on the shape of the detection function and whether or not it is practical to collect perpendicular distance or radial distance with the corresponding angle. If it is not practical to collect distance data, and there is reason to believe that the detection function has a broad shoulder (e.g. on the basis of preliminary data) an investigator may choose to use strip rather than line transect sampling. However if there is significant detection probability outside of the area where detection is 100%, then strip transect methods consistently underestimate true population size [22,23,24] This is the situation of an observer counting organisms from a manned submersible. If data on the perpendicular distance is available, then line transect sampling is probably preferable.

Line transect In line transect sampling, the visibility of an organism is assumed to decline with its perpendicular distance from the transect center line. For each animal, the perpendicular distance or radial distance and corresponding angle off the transect center line are recorded (perpendicular distance can be estimated from radial distance and angle). The probability of detection versus distance off the transect center line is modeled, and the resulting function is used to estimate an effective strip width. There are a number of critical assumptions in line transect sampling: 1) the probability of detecting an organism on the transect center line is unity, 2) organisms are randomly distributed, 3) organisms are moving slow with respect to the camera, 4) each count is independent and no organism is counted more than once, and 5) distances and angles are measured without error [19]. Line transect sampling has been used in a limited number of instances to census objects on sea or lake floors [24,25,26].

We will use the still camera data from the previous section as an example of the application of line transect sampling in the analysis of data from camera surveys of demersal fishes on the sea floor. It should be noted that the distribution of "sightings" of fish in photographs only approximates the case of analyzing continuous video footage.

In line transect sampling, the density of organisms can be estimated by the following equation:

$$D = n\ f(0)/2L$$

where n is the total number of organisms counted, and L is the length of the transect. The parameter f(0) is related to the probability of detecting an organism on the transect center line by the following equation;

$$f(x)=g(x)/a$$

where

$$g(x)=\Pr(\text{object observed}|x)$$

and x is the perpendicular distance from the transect center line and

$$a=1/f(0)$$

is one half the effective strip width [19].

A number of models have been used to analyze line transect data (e.g. Fourier series, hazard-rate; [18]). We have used the hazard-rate model to predict effective strip widths for the four cases represented in Figure 2. The probability density functions are similar in shape, but differ in the effective strip width. For *Eptatretus* occupying burrows, effective strip width was narrower than for the other 3 cases. For *Microstomus pacificus*, the probability of detection does not decrease monotonically with distance from the transect center line, but shows a peak at 50 cm. This suggests that this species is moving in response to the camera sled. If video rather than still photography had been used it would have been possible to observe this behavioral response. In video transects with the ROV, we have observed *Microstomus pacificus* moving in response to the approaching ROV.

CONCLUDING REMARKS

Observer and video transects provide an opportunity to analyze the association of fishes with physical and biological features in their environment. This can be either an association with physical features, such as habitat type and substrate, or with biological features, such as prey complexes. Observer and video transects contain extremely valuable qualitative data that often is very important in forming hypotheses about the processes which control community structure. The information about the biology of these organisms obtained from these surveys should help explain their distributions and therefore reduce the large variances of their population estimates.

There are different operational considerations for *in situ* surveys (either observer or video transects), and for trawl surveys. Each method has some advantage over the other.

Observer transects have some advantages over video transects such as 1) a wider field of view, 2) the human eye has better resolution and is more sensitive at low light levels than the camera, 3) human observers have a much greater depth of field and bionocular vision, and 4) most important, with observer transects there is immediate interaction between the viewing and decision making process. However, the cost of observer data obtained with manned submersibles is much higher than video data obtained from an ROV.

Video surveys obtained from either manned submersibles or ROVs provide a permanent record of organisms and their associations with the substrate. Video data is ideally suited for analysis using line transect techniques.

Trawls typically integrate a larger area of sea floor for a given expenditure of time. In addition trawls provide specimens that are essential for additional studies such as reproduction and feeding. However, trawling is limited to smooth substrate and population estimates based on samples from only one habitat may be erroneous. When used in conjunction with video transects, trawl caught specimens can be invaluable in confirming identifications.

SUMMARY

Visual line transect estimates of fish populations have great potential for fisheries management, both for reducing the very large variances around the population estimates and for providing qualitative data that is important in forming hypotheses about how these communities work. The reliability of these systems must be improved. ROV video transects are the most useful method because of the large sample size required and because the cost of observer line transects are prohibitive, when large, manned submersibles are used. Some trawl component of surveys may be necessary to provide sample material and ground truth referencing.

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REFERENCES

1 Pope, J.G. 1972. An investigation of the accuracy of virtual population analysis using cohort analysis. Int. Comm. North. Atlantic Fish., Res. Bull. 9:65-74.

2 Methot, R.D. 1990. Synthesis model: An adaptable framework for analysis of diverse stock assessment data. Inter. North Pacific Fish. Comm. 50:259-278.

3 Lenarz, W.H. and P.B. Adams. 1980. Some statistical considerations of the design of trawl surveys for rockfish (Scorpaenidae). Fish. Bull., U.S. 78:659-674.

4 Raymore, P.A. and K.L. Weinberg. 1990. 1984 spring and autumn surveys of Pacific west coast upper continental slope groundfish resources. NOAA Tech. Memo. NMFS F/NWC-179, 196 pp.

5 Pennington, M. 1986. Some statistical techniques for estimating abundance indices from trawl studies. Fish. Bull., U.S. 84(3):519-525.

6 Hecker, B. 1990. Variation in megafaunal assemblages on the continental margin south of New England. Deep-Sea Res. 37: 37-57.

7 Etchemendy, S. 1990. Requirements for optimal lighting for visual data acquisition DSV 2 Alvin. Unpublished MS.

8 Olsson, M. 1989. ROV lighting with metal halide. Intervention 89: 182-190.

9 Tusting, R. F., F. M. Caimi, and L. D. Taylor. Special-purpose illumination systems for remotely operated vehicles. Intervention 89: 170-175.

10 Davis, D. L. and R. F. Tusting. 1991. Quantitative benthic photography using laser calibrations. Conf. Proc. Undersea World 91. San Diego.

11 Grassle, J. F., H. L. Sanders, R. R. Hessler, G.T. Rowe, and T. McLellan. 1975. Pattern and zonation: a study of the bathyal megafauna using the research submersible Alvin. Deep-Sea Res. 22: 457-481.

12 Uzmann, J. R., R. A. Cooper, R. B. Theroux, and R. L. Wigley. 1977. Synoptic comparison of three sampling techniques for estimating abundance and distribution of selected megafauna: submersible versus camera sled versus otter trawl. Mar. Fish. Rev. 39: 11-19.

13 Rowe, G. T. 1983. Biomass and production of the Deep-sea macrobenthos, p 97-121. *In* G. T. Rowe [ed.], The Sea: Deep-sea Biology, Wiley

14 Young, D. K., W. H. Jahn, M. D. Richardson, and A. W. Lohanick. 1985. Photographs of deep-sea lebensspuren: a comparison of sedimentary provinces in the Venzuela Basin, Caribbean Sea. Mar. Geol. 68: 269-301.

15 Wakefield, W. W. and A. Genin. 1987. The use of a Canadian (perspective grid) in deep-sea photography. Deep-Sea Res. 34: 469-478.

16 Kaufmann, R. S., W. W. Wakefield, A. Genin. Distribution of epibenthic megafauna and lebensspuren on two central North Pacific seamounts. Deep-sea Res. 36:1863-1896.

17 Wakefield, W. W. Patterns in the distribution of demersal fishes on the upper Continental Slope off Central California with studies on the role of ontogenetic vertical migration in particle flux. Phd. Thesis Scripps Institution of Oceanography, University of California, San Diego, 280pp.

18 Buckland, S. T. 1985. Perpendicular distance models for line transect sampling. Biometrics 41: 177-195.

19 Burham, K. P., D. R. Anderson and J. L. Laake. 1980. Estimation of density from line transect sampling of biological populations. Wildlife Monographs 72. 202 p.

20 Seber, G. A. F. 1982. The estimation of animal abundance and related parameters, 2nd edition. MacMillan, New York.

21 Hiby, A. R. and P. S. Hammond. 1989. Survey techniques for estimating abundance of cetaceans. Rep. Int. Whal. Commn. (Special Issue II).

22 Thresher, R. E. and J. S. Gunn. 1976. Comparative analysis of visual techniques for highly mobile, reef associated piscivores (Carangidae). Environ. Biol. Fish. 17:93-116.

23 Witzig, J. F. 1988. The visual assessment of reef fish communities. Phd. Thesis. North Carolina State Univ. Chapel Hill, North Carolina. 187 p.

24 Bergstedt, R. A. and D. R. Anderson. 1990. Evaluation of line transect sampling based on remotely sensed data from underwater video. Trans. Amer. Fish. Soc. 119:86-91.

25 Wigley, R. L, R. B. Theroux, and H. E. Murray, 1975. Deep-sea crab, *Geryon quinquedens*, survey off northeastern United States. Mar. Fish. Rev. 37: 1-21.

26 Patil, G. P., Taillie, C. and R. L. Wigley. 1980. Transect sampling methods and their application to the deep-sea red crab. pp. 493-504. *in* Advanced Concepts in Ocean Measurements for Marine Biology. F. P. Diemer, F. J. Verhberg and D. Z Mirkes, eds. U. South Carol. Press. Columbia, S. C.

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Chlorinated Hydrocarbon Concentrations and Their Use for Describing Population Discreteness in Harbor Porpoises from Washington, Oregon, and California

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ABSTRACT

Concentrations of PCB (polychlorinated biphenyls, a class of industrial chemicals), DDE (the primary breakdown product of the pesticide DDT), and HCB (hexachlorobenzene, a fungicide) were determined in blubber samples from 45 harbor porpoises collected along the coasts of Washington, Oregon, and California. The primary purpose of this study was to test for regional patterns in the concentration of contaminants and their ratios in order to evaluate the feasibility of using contaminants to gain information about the degree of intermixing of harbor porpoises along the west coast of North America. Concentrations varied widely with averages of 14 ppm (mg/kg by wet weight) PCBs, 31 ppm DDE, and 0.51 ppm HCB. Concentrations of contaminants were strongly associated with latitude (location), length of the animal, and sex. Distinct regional patterns were found in both the concentrations of DDE and the ratios of PCB to DDE and HCB to DDE. Contaminant ratios were far less variable than individual contaminant concentrations and were, therefore, more useful for examining regional patterns. Through discriminant analysis using a combination of pollutant ratios, the state (California, Oregon, or Washington) in which harbor porpoises were collected could be correctly predicted for 86% of the samples. Pollutant ratios did not reveal specific boundaries for stocks but indicated that harbor porpoise movements may be restricted in some areas.

Introduction

Chlorinated hydrocarbon contaminants have been recovered from marine mammals from around the world (Gaskin et al. 1971; Taruski et al. 1975; Clausen et al. 1974; Wagemann and Muir 1984). Risebrough (1978) reviewed the occurrence and impacts of pollutants in marine mammals. Nearshore marine mammals such as pinnipeds and some cetaceans tend to accumulate high concentrations of stable chlorinated hydrocarbons because they 1) are long lived, 2) feed high on the food chain, and 3) have blubber layers that serve as stable repositories for these lipophilic contaminants.

Harbor porpoise (*Phocoena phocoena*) occur primarily in nearshore waters off Europe, Asia, and the east and west coasts of North America (Gaskin et al. 1974). Harbor porpoise populations have declined in many parts of their range (Otterlind 1976; Prescott and Fiorelli 1980; Calambokidis et al. 1984), and there is evidence of high rates of mortality in nets along the California coast (Deiter 1991; Diamond and Hanan 1986; Hanan et al. 1986). Estimates of harbor porpoise population size along the west coast of the United States have recently been completed (Barlow 1988) but there is little information on the presence of different population stocks or interchange among areas.

The potential utility of chlorinated hydrocarbon concentrations or ratios for examining movements and intermixing in marine mammals has been reported previously (*see* review in Aguilar 1987). Winn and Scott (1978) included differences in PCB and DDT concentrations as part of the

In Marine mammal strandings in the United States: proceedings of the Second Marine Mammal Stranding Workshop; 3-5 December 1987, Miami, Florida (John E. Reynolds III and Daniel K. Odell, eds.). NOAA Technical Report NMFS 98 (1991).

Table 1
Sources of harbor porpoise samples analyzed in this study.

Sources	Region	Years collected	No. of samples	Sample prefix
Wa. Dept. Game Olympia, WA	Wash. and N. Ore.	1981–85	4	MMP and WDG
Nat. Mar. Mamm. Lab Seattle, WA	N. Wash.	1984	1	RJF
Cascadia Research Olympia, WA	N. Wash.	1985	4	CRC
Oregon State Univ. Newport, OR	Oregon	1984–86	8	OSU
Ore. Inst. Mar. Biol. Coos Bay, OR	Oregon	1985–86	4	OIMB and UO
Cal. Acad. Sci. San Francisco, CA	Cent. Calif.	1971–86	4	CAS
SW Fisheries Center La Jolla, CA	Cent. Calif.	1983–85	18	LML, REJ, MVZ, and MLML
Nat. Hist. Mus. of LA Co. Los Angeles, CA	S. Calif.	1983	2	JEH

evidence for separate stocks of humpback whales in the western North Atlantic. Gaskin et al. (1982) noted differences in DDT concentrations in harbor porpoises from inside and outside the Bay of Fundy. Calambokidis et al. (1984; 1979a) reported differences in the PCB/DDE ratio in Washington harbor seals and discussed its usefulness in evaluating regional movement and interchange.

The purposes of this study were to 1) determine the concentrations of PCBs (polychlorinated biphenyls, a class of industrial chemicals), DDE (the primary breakdown product of the pesticide DDT), and HCB (hexachlorobenzene, a fungicide) in harbor porpoises from Washington, Oregon, and California; 2) test for regional differences in these contaminants and their ratios; and 3) evaluate the utility of this information in discerning harbor porpoise populations.

Methods

Blubber samples from 45 harbor porpoises were tested for concentrations of PCBs, DDE, and HCB. Also, seven blubber samples were taken from different locations (anterior-dorsal, mid-dorsal, posterior-dorsal, anterior-ventral, mid-ventral, posterior-ventral, and mid-lateral) from each of two harbor porpoises for testing to evaluate toxicant differences based on body location.

Sample Collection

Samples for analysis were received from a wide variety of sources in addition to those collected by the authors (Table 1). All were collected from animals found dead on the shores of Washington, Oregon, and California (Fig. 1). Samples were stored either in glass, aluminum foil, or plastic bags. Samples were stored frozen after collection, except those provided by the California Academy of Science, which had been preserved in formalin. Cooperating organizations also provided information that was tested for association with contaminant concentrations, including collection location, date, sex, length, and blubber thickness.

Sample Analysis

Analyses for concentrations of PCBs, DDE, and HCB were conducted as described in previous reports (Calambokidis et al. 1979b, 1984; Mowrer et al. 1977). The analyses were conducted at the Environmental Analysis Laboratory of The Evergreen State College.

Approximately 5 g of blubber, subsampled from the unexposed interior of samples received, was digested in 50 mL BFM solution (glacial acetic and perchloric acid) over a steam bath for several hours (Stanley and LeFavoure 1965). Samples were extracted four times with 20 mL aliquots of 'pesticide quality' hexane. Lipid weights were determined by evaporating a portion of the hexane-lipid extract to dryness. A 10 mL portion of the hexane-lipid extract was cleaned with 1–2 mL concentrated sulfuric acid (Murphy 1972). After centrifuging, 1–9 μL was injected into a Hewlett-Packard electron capture (63Ni) gas chromatograph equipped with a 1/4″ × 6′ glass column packed with 10% DC-2OO on Gas Chrom Q, 80/100 mesh. The column also had a 1″ alkaline (KOH and

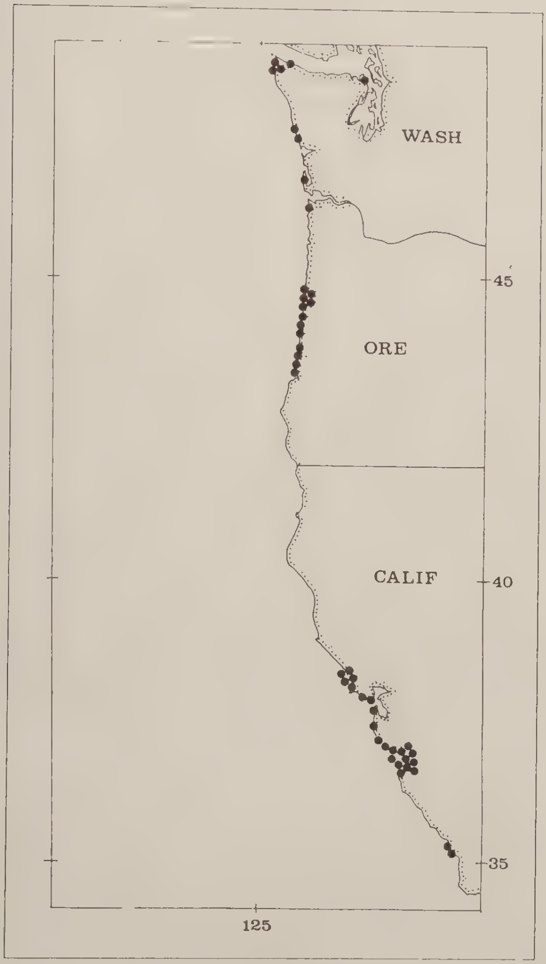

Figure 1
Locations of strandings of harbor porpoises sampled for this study.

NaOH) precolumn to reduce interference from other compounds and to convert any small amounts of p,p′DDT to p,p′DDE (Miller and Wells 1969). The concentration of p,p′DDE plus any p,p′DDT will be referred to as DDE throughout this paper.

Contaminants were identified and quantified based on comparison of elution times and peak areas to PCB, DDE, and HCB standards injected daily. PCBs (a mixture of compounds) were quantified by individual homolog analysis using mean weight percent figures reported by Webb and McCall (1973). Minimum PCB values were calculated using only the more chlorinated PCB homologs corresponding to the PCB components present in the commercial PCB mixture Aroclor 1260. Though additional less chlorinated PCB homologs were present, they were not included in the total because some samples contained interfering compounds and a reproducible minimal value was considered more important than a more variable estimate of total PCBs. The magnitude of this downward bias is approximately 25–40%.

Multiple linear regression and ANOVA were used to evaluate the association between contaminant concentrations and other variables. Concentrations based on lipid weight were used for the linear regressions because lipid weight was found to be significantly correlated to concentrations in models using wet weight. Concentrations were log transformed for these calculations to meet the assumptions of normal distribution of data. In addition to latitude, collection location was categorized by state and five collection locations: the Morro Bay, CA area ($n = 2$); the Monterey Bay, CA area ($n = 13$); the San Francisco/Bodega Bay, CA ($n = 9$); Oregon ($n = 13$); and Washington ($n = 8$). (More detail was included in California owing to high fishery mortality there.) Two samples were excluded from multivariate tests: one collected 10 years prior to the other samples and the other collected within the inland waters of Puget Sound, Washington.

Stepwise discriminant analysis and stepwise multiple regression were used to determine whether collection locations could be predicted from linear combinations of pollutant values. Discriminate analysis was formed using collection location as the categorical variable. A jackknifed calculation system was used to determine the predictive power of discriminant functions (Lachenbruch and Mickey 1968). Each sample was classified based on discriminant functions calculated from all data excluding the sample being classified. Multiple regression was performed using latitude of the recovered sample as the dependent variable. Five predictive variables were considered (all expressed as ratios): PCB/DDE, HCB/DDE, PCB-14/PCB, PCB-16/PCB, and PCB-17/PCB. The PCB-14, PCB-16, and PCB-17 components represent homologs of PCB that comprise a portion of the total PCBs quantified. The DDE was chosen as the denominator for the first two variables because it showed lower coefficient of variation than did PCBs or HCB. Because the variables were expressed as ratios, the assumption of homogeneity of variance is violated. For this reason, more emphasis will be placed on the descriptive aspects of multivariate analyses, and little emphasis will be given to significance tests. Multivariate and discriminant statistical tests were performed using SYSTAT (Wilkinson 1986) and BMDP (Dixon 1985) computer programs.

Results

Concentrations of PCBs, DDE, and HCB in the blubber of the 45 harbor porpoises examined varied widely (Tables

Table 2

Description of and results for harbor porpoise blubber samples from California.

		Collection date							Concentration (mg/kg, wet wt.)			Ratios		
Sample #	Latitude (degrees)	(d)	(mo)	(yr)	Sex	Standard length (cm)	Blubber thickness (cm)	% lipid	PCB	DDE	HCB	PCB/ DDE	HCB/ DDE	HCB/ PCB
JEH-338	35.4	27	09	1983	F	138	1.0	76	16.3	85.2	0.77	0.19	0.0091	0.047
JEH-339	35.5	17	08	1983	M	134	1.5	73	22.1	131.8	0.58	0.17	0.0044	0.026
LML-85-4A	36.65	27	02	1985	F	135	2.2	83	7.5	25.1	0.34	0.30	0.0134	0.045
LML-85-4B	36.8	11	04	1985	F	149	2.0	78	21.8	65.4	0.52	0.33	0.0079	0.024
MLML-001	36.8	—	—	1985	M	127	2.2	83	9.9	34.2	0.43	0.29	0.0126	0.044
MLML-005	36.8	—	—	1985	M	131	1.5	87	14.8	60.0	0.69	0.25	0.0115	0.047
LML-86-6	36.8	28	07	1986	M	96	1.5	82	11.3	35.7	0.44	0.32	0.0123	0.039
LML-85-8	36.9	14	09	1983	F	117	1.8	83	5.7	15.2	0.31	0.37	0.0204	0.055
LML-84-5	36.9	03	08	1984	F	150	1.3	73	42.0	101.5	0.64	0.41	0.0063	0.015
LML-85-3	36.95	07	03	1985	F	159	2.0	85	10.0	25.6	0.09	0.39	0.0034	0.009
LML-84-3	36.95	13	05	1984	M	77	1.1	69	2.6	6.3	0.07	0.41	0.0105	0.026
LML-85-5	36.95	27	05	1985	F	103	2.0	74	18.1	66.3	0.89	0.27	0.0134	0.049
LML-85-6	36.95	23	08	1985	F	147	2.0	99	12.7	48.7	0.42	0.26	0.0085	0.033
HJB-008	36.95	09	07	1983	F	131	1.6	68	25.6	77.6	0.58	0.33	0.0075	0.023
LML-86-5	37.1	30	05	1986	F	168	2.5	85	7.2	17.6	0.22	0.41	0.0125	0.031
CAS-A3870	37.35	30	06	1984	F	85	1.7	85	8.2	11.5	0.33	0.72	0.0286	0.040
CAS-A3209	37.8	01	07	1980	M	75	1.0	59	8.8	20.3	0.25	0.43	0.0125	0.029
CAS-22173	37.9	27	05	1980	F	80	1.5	48	9.5	13.0	0.11	0.73	0.0086	0.012
CAS-15892	37.9	23	04	1971	F	69	1.0	51	3.2	14.2	0.07	0.23	0.0048	0.021
MVZ-172409	38.3	15	07	1986	F	108	2.0	92	2.1	8.3	0.15	0.26	0.0181	0.070
REJ-1415	38.4	—	—	1985	F	132	1.7	90	5.6	21.9	0.28	0.25	0.0127	0.050
REJ-1414	38.4	08	05	1985	M	145	1.0	51	6.1	26.9	0.16	0.23	0.0059	0.026
MVZ-172408	38.4	15	07	1986	M	162	0.5	49	63.6	101.0	0.38	0.63	0.0037	0.006
MVZ-173468	38.5	20	08	1986	F	154	2.0	81	5.1	14.1	0.12	0.36	0.0085	0.024

2 and 3). Concentrations of PCBs averaged 14 ppm (mg/kg wet weight, SD = 13) or 21 ppm (lipid weight, SD = 23). The DDE concentrations tended to be higher, averaging 31 ppm (wet weight, SD = 30) or 45 ppm (lipid weight, SD = 46). The HCB concentrations were much lower than PCB or DDE averaging 0.51 ppm (wet weight, SD = O.42) or 0.77 ppm (lipid weight, SD = 0.80). Concentrations of DDE (lipid weight, log transformed) varied significantly among the five regions compared (ANOVA, $P<0.001$). No significant differences were found among regions for PCB or HCB (ANOVA, $P>0.05$).

Stepwise multiple regression analyses were used to determine which factors best explained the variations in concentrations found. A significant regression was found between PCBs and animal length ($r = 0.37$, $P<0.05$). The DDE concentrations were significantly associated with length and latitude ($r = 0.51$, $P<0.01$). The HCB concentrations were weakly associated with latitude ($r = 0.39$, $P<0.05$). Blubber thickness and year of collection significantly influenced contaminant concentrations in some models, with higher concentrations associated with thinner blubber layers and earlier collection years. These effects were generally weak or not significant in all models.

The association between PCB and DDE concentrations and length was not consistent for males and females. For both PCBs and DDE the association between concentrations and animal length was significant in males ($n = 17$, $r = 0.70$, $P<0.01$ and $r = 0.76$, $P<0.01$, respectively) but not in females ($n = 26$, $P>0.05$ for both PCB and DDE). The significant associations with length in the entire sample, therefore, primarily reflect this association in males only.

Ratios of contaminants were less varied than the concentrations. Both the ratios of PCB to DDE and HCB to DDE varied significantly by latitude ($r = O.70$, $P<0.001$ and $r = 0.83$, $P<0.001$, respectively). Similarly both these ratios varied significantly among regions (ANOVA, $P<0.001$ in both cases). No significant associations were found between ratios and others factors. Figure 2 illustrates differences in the PCB/DDE ratio among regions.

Analyses of blubber samples from seven different locations on two harbor porpoises (14 samples) yielded similar results. In both animals, samples from the dorsal peduncle area had about 20% lower concentrations than other samples. Concentrations from other parts of the body were fairly uniform deviating less than 10% in most cases (never more than 20%) from average values for all samples (excluding the dorsal peduncle). Further details of this comparison are reported in Calambokidis (1986). Concentrations (by lipid weight) and ratios for four samples pre-

Table 3

Description of and results for harbor porpoise blubber samples from Oregon and Washington.

Sample #	Latitude (degrees)	Collection date			Sex	Standard length (cm)	Blubber thickness (cm)	% lipid	Concentration (mg/kg, wet wt.)			Ratios		
		(d)	(mo)	(yr)					PCB	DDE	HCB	PCB/ DDE	HCB/ DDE	HCB/ PCB
Oregon														
OIMB-C044	43.4	04	07	1986	F	90	1.0	62	2.8	9.5	0.54	0.30	0.0570	0.192
OIMB-C043	43.45	11	07	1986	M	70	0.5	57	1.9	6.9	0.21	0.27	0.0300	0.110
UO-1	43.7	19	03	1985	F	115	—	60	2.2	3.0	0.16	0.73	0.0530	0.073
OIMB-C046	43.9	25	07	1986	F	92	0.5	55	1.4	3.2	0.16	0.45	0.0490	0.111
OSU784-256	44.4	27	07	1984	F	149	1.6	80	11.5	33.2	0.64	0.35	0.0190	0.055
OSU886-764	44.45	21	08	1986	M	149	1.0	57	12.4	28.0	0.47	0.44	0.0167	0.038
OSU786-761	44.6	07	07	1986	F	172	1.5	84	1.5	2.1	0.08	0.70	0.0370	0.054
OSU786-762	44.65	11	07	1986	F	178	1.4	84	2.7	4.7	0.31	0.58	0.0660	0.113
OSU785-658	44.65	15	07	1985	M	159	1.5	85	13.5	32.0	0.51	0.42	0.0160	0.038
OSU784-255	44.65	24	07	1984	M	118	1.5	67	5.7	18.5	0.92	0.31	0.0500	0.162
OSU985-679	44.7	14	08	1985	F	103	—	41	22.9	38.3	1.76	0.60	0.0460	0.077
OSU885-671	44.7	10	08	1985	M	121	2.0	80	13.5	17.7	0.84	0.76	0.0470	0.062
MMP-108	45.9	06	04	1981	M	141	2.0	69	49.6	52.1	1.78	0.95	0.0342	0.036
Washington														
MMP-92	46.7	06	03	1981	M	131	2.0	82	29.9	26.7	0.87	1.12	0.0327	0.029
MMP-SKULL	47.3	04	09	1985	—	120	1.0	19	6.6	10.0	0.43	0.66	0.0436	0.066
MMP-384	47.3	20	09	1985	—	—	—	15	0.2	0.2	0.01	1.02	0.0490	0.048
RCF-112	48.2	26	07	1984	F	176	1.7	85	26.6	15.2	0.56	1.75	0.0370	0.021
CRC-251	48.6	11	08	1985	F	142	1.1	85	22.3	12.5	0.91	1.78	0.0730	0.041
CRC-250	48.6	11	08	1985	M	163	2.0	80	28.1	16.3	0.72	1.72	0.0440	0.026
CRC-248	48.6	11	08	1985	F	171	1.5	79	8.7	7.6	0.42	1.13	0.0550	0.049
CRC-308	48.2[a]	25	04	1986	M	124	0.8	66	15.8	26.7	1.73	0.59	0.0647	0.109

[a] Collected from Puget Sound, Washington.

served in formalin were not significantly different from those that had been frozen (ANCOVA, $P>0.05$, with all other significant factors used as covariates).

Stepwise discriminant analysis was based on five predictive variables and data collected from five locations. The three variables, which included the fractional composition of total PCBs did not, however, add appreciably to the discrimination of collection location and were excluded by the stepwise procedure. Using only two variable (PCB/DDE and HCB/DDE) discriminant analysis, we were able to assign correct collection location to 63% of 43 samples (Table 4). On a coarser geographic scale, 86% of samples were correctly assigned to state (Table 4). Typically with discriminant analysis, the separation of groups is illustrated by plotting the first and second factor scores for each sample. When only two variables are used to compute the factor scores, it is equivalent to plotting the values for each variable (Fig. 3; note that a plot of factor scores would be a simple rotation of this figure). As seen in Figure 3, there are three samples taken in Oregon which appear to be more similar to California samples, and there is one sample from Washington which appears similar to Oregon samples. Within California, the southern samples appear relatively distinct from other areas, but there is considerable overlap between Monterey Bay and areas north of there. Samples from Monterey Bay are characterized by very low variance in both PCB/DDE and HCB/DDE ratios (Fig. 3).

Multiple regression was able to predict accurately the latitude at which samples were collected using 5 variables (multiple R = 0.89). Again the fractional components of PCBs did not add appreciably to the regression and were excluded by the stepwise procedure. The regression coefficient (multiple R) was 0.87 using only PCB/DDE and HCB/DDE. The predicted and estimated latitudes for each sample are shown in Figure 4. There appear to be four outliers in Oregon which appear more like those from northern California and one sample from California that appears more like those from southern Oregon.

Discussion

Concentrations of chlorinated hydrocarbons found in this study were generally in the middle of the range reported from harbor porpoises from other areas (Gaskin et al. 1971; 1982; Koeman et al. 1972; Clausen et al. 1974; Otterlind 1976; Calambokidis et al. 1984). Correlations between length and contaminant concentrations found in this study

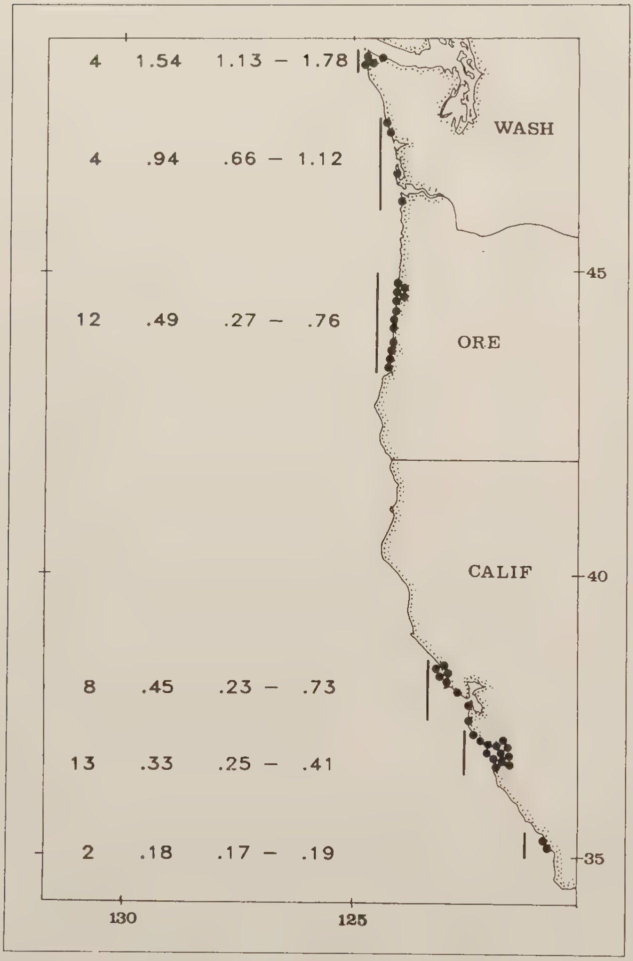

Figure 2
Number of samples, mean, and range of PCB/DDE ratios for harbor porpoises from different areas. Excluded are one sample collected in 1971 and one sample from Puget Sound (inland waters of Washington State).

Table 4
Predicted sample locations from discriminant analysis using PCB/DDE and HCB/DDE as predictive variables. Samples were categorized as being from Morro Bay Area (CA-1), Monterey Bay (CA-2), San Francisco/Bodega Bay area (CA-3), Oregon (OR), and Washington (WA). Excluded are one sample collected in 1971 and one from Puget Sound (inland waters of Washington State). A total of 27 locations were predicted correctly to region and 37 were predicted correctly to state (out of [illegible] samples).

Actual collection location	Predicted collection location					
	CA-1	CA-2	CA-3	OR	WA	Total
CA-1	2	0	0	0	0	2
CA-2	1	7	5	0	0	13
CA-3	1	3	3	1	0	8
OR	0	1	2	9	1	13
WA	0	0	0	1	6	7
Total	4	11	10	11	7	43

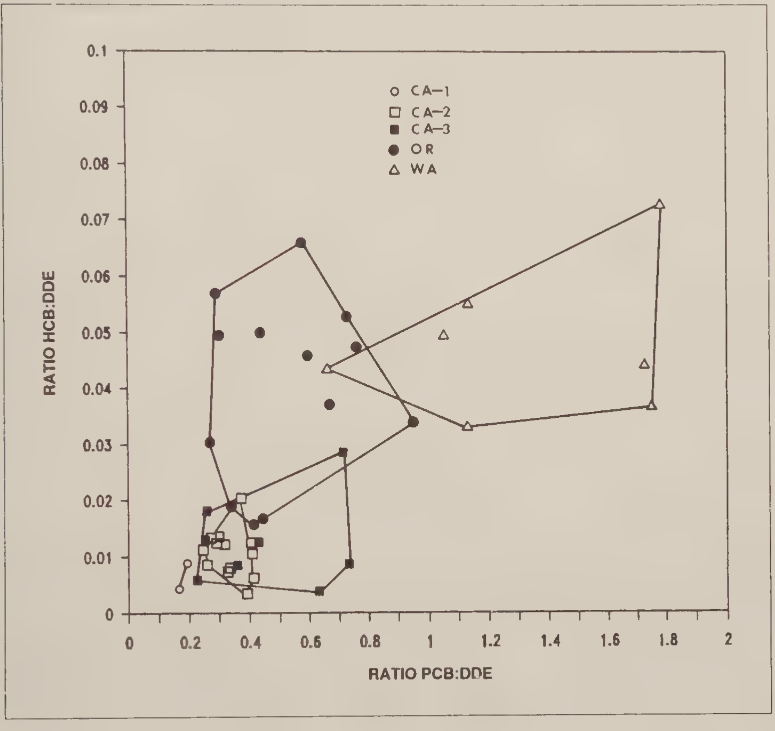

Figure 3

Pollutant residues expressed as the ratios HCB/DDE and PCB/DDE for 43 samples collected in 5 regions. Regions are defined in the text. Polygons enclose all samples collected in each of the 5 regions.

are consistent with other reports of accumulation with age primarily in male harbor porpoises (Gaskin et al. 1982; 1983) and other marine mammals (Addison et al. 1973; 1983) and other marine mammals (Addison and Smith 1974; Donkin et al. 1981; Calambokidis et al. 1984).

Organic pollutant residues give valuable clues regarding the population structure and feeding ecology of west-coast harbor porpoises. If the population were panmictic (randomly mixing), homogeneous pollutant ratios for all samples should exist. Instead, very strong gradients occur with latitude. This is likely to occur only if individual porpoises remain in one area for long periods of time. Similarly, pollutant ratios imply something about the feeding ecology of west-coast harbor porpoises. The observed patterns would not be expected if harbor porpoises were feeding on fish populations which had homogeneous pollutant ratios. It is likely that harbor porpoises feed largely on local fish stocks rather than on highly migratory fish. These patterns appear to differ from those of harbor porpoises along the east coast of the United States which may migrate a considerable distance to feed on a migratory fish, the herring, in the Bay of Fundy (Gaskin et al. 1985).

If an individual changes location, it is not known how much time is required to attain pollutant ratios which are characteristic of the new location. The required time period is related to the residence times of the pollutant and the difference between current pollutant load and that characteristic of the new location. Because chlorinated hydrocarbons accumulate over prolonged periods of time (the entire lifespan in males), we infer that most harbor porpoises remain in a region for extended periods if not most of their lives. Some exceptions may be evident in the data. Both discriminant and multivariate regression analyses identified several individuals from Oregon whose pollutant ratios more closely resembled samples from northern California. Although this could be natural variation about a mean value for Oregon, it could also be due to animals that moved at one point during their lives from California to Oregon or to animals that regularly move between those regions.

Pollutant ratios in Monterey Bay samples are particularly interesting because of their low variance. Monterey Bay samples show little variability in both PCB/DDE and HCB/DDE ratios (Fig. 3). Samples collected north of Monterey Bay (primarily near San Francisco and Bodega Bay) overlap with those values seen in Monterey Bay, but have much higher variance. In the discriminant analysis, 62% of the misclassifications were associated with this San Francisco/Bodega Bay area (Table 4). The low variance may be indicative of a resident population in Monterey

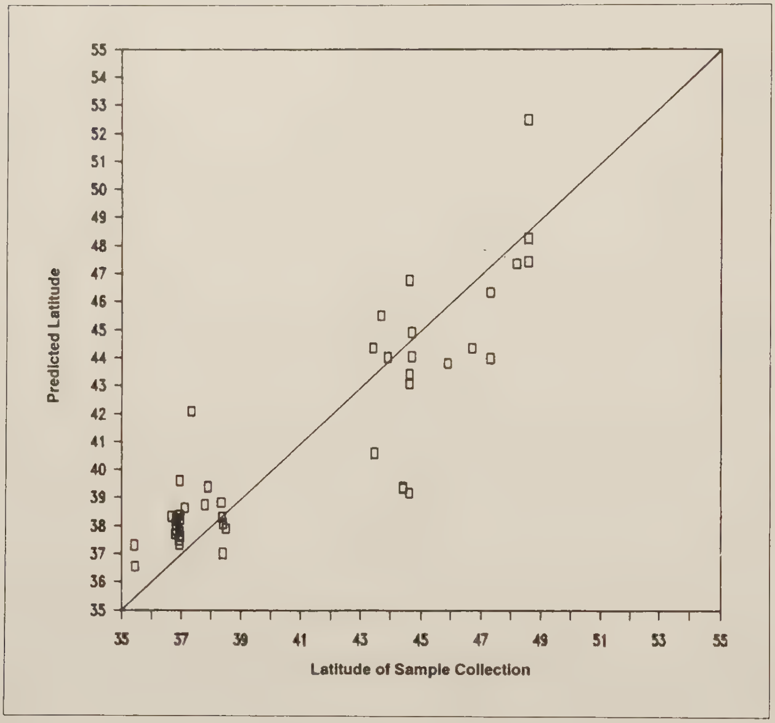

Figure 4
Observed and predicted collection latitudes for 43 samples based on multiple regression. The dependent variables included HCB/DDE and PCB/DDE.

Bay. The higher variance of the more northerly samples may indicate an area of mixing. Although speculative, these interpretations could be tested as additional information becomes available.

Unfortunately, pollutants ratios do not indicate any logical subdivision of the west-coast porpoise population into stock units. A stock is a management term and does not have a widely accepted definition. The Marine Mammal Protection Act of 1972 defines a stock as a group of animals of the same species which inhabit a common spatial arrangement and which interbreed when mature. Perhaps the best definition of a stock is a collection of animals that can be sensibly managed as a single unit (Larkin 1972; MacCall 1984). The problem with harbor porpoise management is that the animals do not appear to fit this concept of a stock. Based on pollutant ratios, harbor porpoises do not move great distances; thus animals from California and Washington are not likely to interbreed and should thus be assigned to different stocks. However, there may be movement from Washington to Oregon and from northern California to Oregon. Harbor porpoise distributions are continuous between California and Washington (Barlow 1988) and there are no apparent barriers to movement or gene exchange. Thus assigning clear boundaries of potentially discrete stocks may not be possible.

It is unrealistic to expect that one technique, analysis of pollutant ratios, will answer all questions about stock structure. We have suggested, however, that harbor porpoise interchange between some areas is relatively restricted. Other techniques, such as conventional tagging or radio tracking may help refine knowledge of their movements and use of cytogenetic and biochemical methods (*see* Duffield et al. 1991) may determine degree of interbreeding. Until such additional information becomes available, we urge a conservative approach to harbor porpoise management, avoiding depletion of populations in local areas.

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Citations

Addision, R.F., and T.G. Smith.
1974. Organochlorine residue levels in Arctic ringed seals: variation with age and sex. Oikos 25:335-337.

Addison, R.F., S.R. Kerr, J. Dale, and D.E. Sergeant.
1973. Variation of organochlorine residue levels with age in Gulf of St. Lawrence harp seals (*Pagophilus groenlandicus*). J. Fish. Res. Board Can. 30:595-600.

Aguilar, A.
1987. Using organochlorine pollutants to discriminate marine mammal populations: a review and critique of the methods. Mar. Mammal Sci. 3:242-262.

Barlow, J.
1988. Harbor porpoise, *Phocoena phocoena*, abundance estimation for California, Oregon and Washington: I. ship surveys. Fish. Bull., U.S. 86:417-432.

Calambokidis, J
1986. Chlorinated hydrocarbons in harbor porpoise from Washington, Oregon, and California: regional differences in pollutant ratios. NMFS Southwest Fish. Cent. Adm. Rep. LJ-86-35C. 29 p.

Calambokidis, J., S. Carter, and J.C. Cubbage.
1979a. The concentrations and dynamics of chlorinated hydrocarbon contaminants in harbor seals and their use in gaining biological information. *In* Proceedings (abstracts) of the third biennial conference on the biology of marine mammals; 7-11 October 1979, Seattle, WA.

Calambokidis, J., J. Mowrer, M.W, Beug, and S.G. Herman.
1979b. Selective retention of polychlorinated biphenyl components in the mussel (*Mytilus edulis*). Arch. Environ. Contam. Toxicol. 8:299-308.

Calambokidis, J., J. Peard, G.H. Steiger, J.C. Cubbage, and R.L. Delong.
1984. Chemical contaminants in marine mammals from Washington State. NOAA Tech. Memo. NOS OMS 6. Dep. Commer., NTIS, Springfield, VA. 167 p.

Clausen, J., L. Braestrup, and O. Berg.
1974. The content of polychlorinated hydrocarbons in Arctic mammals. Bull. Environ. Contam. Toxicol. 11:529-534.

Deiter, R.L.
1991. Recovery and necropsy of marine mammal carcasses in and near the Point Reyes National Seashore, May 1982-March 1987. *In* Marine mammal strandings in the United States: proceedings of the second marine mammal stranding workshop; 3-5 December 1987, Miami, FL (J.E. Reynolds and D.K. Odell, eds.), p. 123-141. Dep. Commer., NOAA Tech. Rep. NMFS 98.

Diamond, S.L., and D.A. Hanan.
1986. An estimate of harbor porpoise mortality in California set net fisheries April 1, 1983 through March 31, 1984. NMFS-SWR, Adm. Rep. SWR-86-15, 40 p.

Dixon, W.J. (editor).
1985. BMDP statistical software. Univ. Calif. Press, Berkeley, CA, 734 p.

Donkin, P., S.V. Mamm, and E.I. Hamilton.
1981. Polychlorinated biphenyl, DDT, and dieldrin residues in grey seal (*Halichoerus grypus*) males, females, and mother-foetus pairs sampled at the Farne Islands, England, during the breeding season. Sci. Total Environ. 19:121-142.

Duffield, D.A., J. Chamberlin-Lea, J.C. Sweeney, D.K. Odell, E.D. Asper, and W.G. Gilmartin.
1991. Use of corneal cell culture for R-band chromosome studies on stranded cetaceans. *In* Marine mammal strandings in the United States: proceedings of the second marine mammal stranding workshop; 3-5 December 1987, Miami, FL (J.E. Reynolds and D.K. Odell, eds.), p. 91-100. Dep. Commer., NOAA Tech. Rep. NMFS 98.

Gaskin, D.E., M. Holdrinet, and R. Frank.
1971. Organochlorine pesticide residues in harbour porpoises from the Bay of Fundy region. Nature 233:499-500.
1982. DDT residues in blubber of harbour porpoise, *Phocoena phocoena* (L.) from eastern Canadian waters during the five-year period 1969-1973. Mammals in the Seas, FAO Fish. Ser. No. 5, 4:135-143.

Gaskin, D.E., P.W. Arnold, and B.A. Blair.
1974. *Phocoena phocoena*. Mammalian Species No. 42:1-8.

Gaskin, D.E., R. Frank, and M. Holdrinet.
1983. Polychlorinated biphenyls in harbor porpoise *Phocoena phocoena* (L.) from the Bay of Fundy, Canada and adjacent waters, with some information on chlordane and hexachlorobenzene levels. Arch. Environ Contam. Toxicol. 12:211-219.

Gaskin, D.E., A.J. Read, P.F. Watts, and G.J.D. Smith.
1985. Population dispersal, size, and interactions of harbour porpoises in the Bay of Fundy and Gulf of Maine. Can. Tech. Rep. Fish. Aquat. Sci. 1291:1-28.

Hanan, D.A., S.L. Diamond, and J.P. School.
1986. An estimate of harbor porpoise mortality in California set net fisheries April 1, 1984 through March 31, 1985. NMFS-SWR Adm. Rep. SWR 86-16, 38 p.

Koeman, J.H., W.H.M. Peters, C.J. Smith, P.S. Tjioe, and J.J.M. De Goeij.
1972. Persistent chemicals in marine mammals. TNO Nieuws 27:570-578.

Lachenbruch, P., and R.M. Mickey.
1968. Estimation of error rates in discriminant analysis. Technometrics 10:1-11.

Larkin, P.A.
1972. The stock concept and management of Pacific salmon. *In* The stock concept in Pacific salmon (R.C. Simon and P.A. Larkin, eds.), (p. 11-15). H.R. MacMillan lectures in fisheries, Univ. British Columbia, Vancouver, B.C.

MacCcall, A.
1984. Review of the biological rationale for identifying subpopulations in fisheries. *In* Identifying fish subpopulations: proceedings of a California sea grant workshop; 27 January 1984, Scripps Inst. Oceanogr., Univ. Calif., San Diego (Dennis Hedgecock, ed), p. 9-13.

Miller, G.A., and C.E. Wells.
1969. Alkaline pre-column for use in gas chromatographic pesticide residue analysis. J. Assoc. Off. Anal. Chem. 52:548-553.

Mowrer J., J. Calambokidis, N. Musgrove, B. Drager, M.W. Beug, and S.G. Herman.
1977. Polychlorinated biphenyls in cottids, mussels, and sediment in Southern Puget Sound, Washington. Bull. Environ. Contam. Toxicol. 18:588-594.

Murphy, P.G.
1972. Sulfuric acid for the cleanup of animal tissues for analysis of acid stable chlorinated hydrocarbon residues. J. Assoc. Off. Anal. Chem. 55:1360.

Otterlind, G.
1976. The harbour porpoise (*Phocoena phocoena*) endangered in Swedish waters. ICES C.M. 1976/N:16.

Prescott, J.H., and D.M. Fiorelli.
1980. Review of the harbor porpoise (*Phocoena phocoena*) in the U.S. Northwest Atlantic. Report to U.S. Marine Mammal Commission, Wash., D.C., 64 p.

Risebrough, R.W.
1978. Pollutants in marine mammals, a literature review and recommendations for research. Marine Mammal Commission, NTIS PB-290728, Wash., D.C., 64 p.

Stanley, R.L., and H.T. LeFavoure.
1965. Rapid digestion and clean-up of animal tissues for pesticide analysis. J. Assoc. Off. Agr. Chem. 48:666-667.

Taruski, A.G., C.E. Olney, and H.E. Winn.
1975. Chlorinated hydrocarbons in cetaceans. J. Fish. Res. Board Can. 32:2205-2209.

Wagemann, R., and D.C.G. Muir.
1984. Concentrations of heavy metals and organochlorines in marine mammals of northern waters: overview and evaluation. Can. Tech. Rep. Fish. Aquat. Sci. No. 1279, 97 p.

Webb, R.G., and A.C. McCall.
1973. Quantitative PCB standards for electron capture gas chromatography. J. Chromatogr. Sci. 11:366-373.

Wilkinson, L.
1986. SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, IL, 822 p.

Winn, H.E., and G.P. Scott.
1978. A model for stock structuring of humpback whales (*Megaptera novaeangliae*) in the western North Atlantic. Draft Record to Int. Whal. Comm.

SC/42/SM45

Sampling Effects on the Estimation of Life History Parameters for Eastern Tropical Pacific Dolphins

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ABSTRACT

Specifications for the collection of life history data from eastern tropical Pacific (ETP) dolphins have recently changed. Specimens are now only collected if a total of more than six animals are killed. For a one-year trial period, a monetary reward system was offered for each specimen with life history data collected. The effect of these changes are examined to determine whether the resultant life history data are biased – a concern expressed at the 1989 International Whaling Commission's Scientific Committee meeting. The collected data are stratified by the new requirements, and the representation of females by reproductive condition, and calves is examined for each strata. Few statistically significant differences between the strata in the representation of animals in the sample were found, and no systematic biases were detected in the representation of specimens in the collection. The monetary reward system resulted in a significant increase in the number of specimens collected.

INTRODUCTION

In order to accurately estimate life history parameters for a population, identification of biases in the data collected is critical. In addition to sampling methods, physiological or behavioral characteristics of the animals themselves, such as segregation by age and sex, reproductive seasonality or geographic variation in the species, may contribute to collection bias (for discussion, see Perrin and Reilly, 1984). The Southwest Fisheries Science Center has been collecting data on dolphin specimens from the eastern tropical Pacific (ETP) for 18 years (for documentation on the collection of life history data see Perrin *et al.*, 1976; Smith, 1979; Perrin and Oliver, 1982). Recently, two changes were implemented in the established sampling protocols in an attempt to improve the quality and quantity of data collected for the estimation of age and reproductive condition by observers on the purse-seine vessels: (1) after June 1987, specimen collection was restricted to sets with more than six animals observed killed (prior to that, observers had been instructed to sample every set, selecting the first animals available); and (2) on 1 October 1988, a monetary reward system was implemented for a one-year trial period. Observers were given bonuses for all specimens with minimum life history data collected (i.e., species identification, sex and total body length); a larger bonus was given if the observer returned gonad and teeth samples for the same specimen.

The IWC Scientific Committee (IWC, 1989) questioned whether the first change in collection criteria might introduce a bias in the estimation of life history parameters. This paper addresses this question and tests whether the introduction of a monetary reward system increased the quantity of data collected.

METHODS

Observers placed aboard US tuna purse-seine vessels by both the US National Marine Fisheries Service (NMFS) and the Inter-American Tropical Tuna Commission (IATTC) collect mortality data on the dolphin species incidentally killed in the yellowfin tuna purse-seine fishery in the ETP. Data collected includes the number of dolphins killed by species for each set and the geographic location of the set. The life history data collected from individual dead animals includes the species, sex, total body length and reproductive condition, if female. Gonads and teeth of both sexes are returned to the laboratory for state of sexual maturity and age to be determined.

Spotted (*Stenella attenuata*), spinner (*S. longirostris*), striped (*S. coeruleoalba*), and common dolphins (*Delphinus delphis*) are the primary target species of the ETP yellowfin tuna purse-seine fishery, and, consequently, the species for which we have most data. For spotted and spinner dolphins, sufficient data are available to analyze the data by geographic stocks (Table 1; for descriptions of stocks, see Perrin *et al.*, 1985).

The fraction of females that were sexually mature and the fraction of mature females that were pregnant, lactating and simultaneously pregnant and lactating for each species were first stratified by kill-per-set (KPS) to reflect the new collection protocol of only sampling sets with more than six animals killed. The first KPS stratum included data from purse-seine sets with 1–6 animals killed, ('small-kill' sets) between 1974 and 1987, the last year 'small-kill' sets were sampled. The second stratum included life history data from sets with ≥ 7 animals killed ('large-kill' sets) collected between 1974 and 1989.

The null hypotheses of no significant temporal trend in the fraction of females in each reproductive state (i.e. mature, pregnant, lactating, and simultaneously pregnant and lactating) were tested for each species, or stock, in small- and large-kill sets ($\alpha=0.05$; linear trends for proportions, Snedecor and Cochran, 1973). If the temporal trend was significant, the null hypotheses of no difference between the regression coefficients for each KPS stratum was tested using a bootstrap procedure. The bootstrap was performed by resampling the raw data and comparing the regression coefficients generated. The null hypothesis was rejected if the observed difference in the regression coefficients was not within the 95% confidence interval. If the temporal trend was not significant for either KPS stratum, the annual data were pooled and the null

Table 1

The statistically significant (S) temporal trends, 1974-89, are indicated in the corresponding cell. The sample sizes are given for each species and stock examined and for each strata of kill-per-set. The column headings for the strata are '< 7' for sets with 1-6 animals killed and '> = 7' for large-kill sets. The fraction mature is calculated as the fraction of all females that are mature from all females for which sexual maturity is known. The fraction pregnant, lactating and simultaneously pregnant and lactating are calculated as the fraction of mature females in each condition. The fraction pregnant and the fraction lactating do not include the simulataneously pregnant and lactating females. Blank cells were tested but the results were not statistically significant.

	Sample size		Fraction mature		Fraction pregnant		Fraction lactating		Fraction pregnant & lactating	
Species + Stock	< 7	> = 7	< 7	> = 7	< 7	> = 7	< 7	> = 7	< 7	> = 7
Spotted										
N. Offshore	1,208	3545		S						S
S. Offshore	84	333		S		S				S
Spinner										
Eastern	174	989		S					*	S
Whitebelly	231	986			S	S		S		
Common										
All stocks	114	548								S
Striped										
All stocks	18	44					insufficient data			

* There were no eastern spinners that were recorded to be simulatneously pregnant and lactating in sets with fewer than seven animals killed.

hypothesis of equal mean proportions for each stratum was tested ($\alpha=0.05$; Fleiss, 1981).

The proportion of calves in the sample was examined by the same two KPS strata. Male and female calves were summed and the proportion calculated on the basis of all male and female specimens collected with total body length (TBL) recorded; TBL is used as the criteria to define a calf. Animals with a TBL $\leq$130cm are considered to be calves. This is the approximate length at one year of age and the beginning of weaning (Perrin *et al.*, 1976). When sufficient data were available, the species were analyzed by geographic stock as detailed previously.

Data collected for years 1979 through 1989 were used to evaluate the effectiveness of the monetary incentive program. Both the NMFS and the IATTC participated in the sampling program during these years. To correspond with the trial period for the incentive plan, each year is defined to begin on 1 October and end on 30 September the following year. The first year of IATTC data collection is 1979, thus 'collection year' 1980 (1 October 1979 – 30 September 1980) is the first year used for the analyses. The collection of minimum life history data, for both male and female specimens, was calculated as a percentage of the total observed kill for each year.

RESULTS

Table 1 summarises the results of the test for temporal trends in the data by species and stock. The life history data for spotted (northern offshore, southern offshore and coastal) and spinner dolphin stocks (eastern, northern whitebelly, southern whitebelly and Costa Rican) were examined separately. Sample sizes were too small for analyses of data on coastal spotted and Costa Rican spinner dolphins. The data for southern whitebelly spinner dolphins were also too few and were combined with the data for northern whitebelly spinner dolphins.

None of the tests to compare regression coefficients rejected the null hypotheses of equal slopes. Of the pooled annual data comparisons conducted when there was no significant temporal trend in the data, only the mean proportions for the fraction of lactating eastern spinner dolphin females were significantly different between the large- and small-kill sets.

With respect to the representation of calves in small- versus large-kill sets, significant differences were found only for northern offshore and eastern spinner dolphins (Table 2). A greater fraction of calves were present in the large-kill set samples.

Observer collection rates of both minimum and full life history data increased significantly in 1989 over the 1988 rate and the mean rate for the 1980s (Table 3; Chi-square, $p<0.001$; Snedecor and Cochran, 1973). The fraction of the observed kill collected with full life history data increased significantly to 0.455 in 1989 from a mean for the 1980s of 0.379 (Chi-square, $p<0.001$; Snedecor and Cochran, 1973).

DISCUSSION

The results indicate that there is no significant effect on the representation of female dolphins by reproductive state in the life history sample when the data were stratified by small– and large-kill sets. Although temporal trends in the fraction of females in each reproductive state were significant for some stocks and species examined, the number of animals killed in the set was not a significant factor in the analytical estimation of life history parameters. Although there was a significant difference in the representation of calves between small- and large-kill sets for both northern offshore spotted dolphins and eastern spinner dolphins, this may be due to the increased power of the trend analyses when the proportions are near 0 or 1 (Nam, 1987).

Table 2

The statistically significant (S) temporal trends, 1974-89, are indicated in the corresponding cell. The sample sizes are given for each species and stock examined and for each strata of kill-per-set. The column headings for the strata are '< 7' for sets with 1-6 animals killed and '> = 7' for large-kill sets. The fraction calves is calculated as the fraction of the total sample of male and female specimens collected with length was recorded. Specimens with length < = 130cm are calves.

	Sample size		Fraction calves	
Species + Stock	< 7	> = 7	< 7	> = 7
Spotted				
N. Offshore	9,498	15,244		S*
S. Offshore	1,246	1,781		S
Spinner				
Eastern	2,227	3,884		S*
Whitebelly	2,474	4,180		
Common				
All stocks	1,135	2,054		
Striped				
All stocks	201	287		

* Indicates that the regression lines for the two groups are significantly different, $\alpha = 0.05$.

Table 3

Fraction of the total observed kill sampled as life history data. The life history data collection includes both male and female specimens with minimum data collected, i.e., species, sex and total body length. The 'full' category is minimum data plus gonads. Data in table is for 'collection' years 1980-89. For example, collection year 1980 is October 1, 1979-September 30, 1980.

Collection year	Observed kill	Life history specimens		Fraction of kill collected as life history	
		Min.	Full	Min.	Full
1980	5,747	1,417	865	0.25	0.15
1981	7,731	1,380	757	0.18	0.10
1982	8,205	1,459	703	0.18	0.09
1983	5,702	1,305	748	0.23	0.13
1984	3,236	1,019	317	0.32	0.10
1985	8,546	2,107	1,026	0.25	0.12
1986	12,883	1,756	996	0.14	0.08
1987	9,852	2,226	1,286	0.23	0.13
1988	12,366	1,990	1,515	0.16	0.12
1989	11,490	3,224	2,695	0.28	0.23
Total	85,758	17,883	10,908	0.21	0.13

The low collection rates of life history data from ETP dolphin species during the 1980s has been discussed by the IWC Scientific Committee (IWC, 1989). Besides the incentive of the collection bonuses, the increased collection rate for collection year 1989 may also have been due to the concentration of effort resulting from the instruction to sample only from sets with ≥7 animals killed. However small-kill sets accounted for an average of 30% of the observed kill during 1979 to 1989 and dropping the latter sampling requirement while keeping the bonus system would probably further increase the life history data sampling rate.

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REFERENCES

Fleiss, J.L. 1981. *Statistical Methods for Rates and Proportions*. 2nd Edn. J. Wiley & Sons, London. 321pp.

International Whaling Commission. 1989. Report of the sub-committee on small cetaceans. *Rep. int. Whal. Commn* 39:117–29.

Nam, J. 1987. A simple approximation for calculating sample sizes for detecting linear trends in proportions. *Biometrics* 43:701–5.

Perrin, W.F. and Oliver, C.W. 1982. Time/area distribution and composition of the incidental kill of dolphins and small whales in the U.S. purse-seine fishery for tuna in the eastern tropical Pacific, 1979–80. *Rep. int. Whal. Commn* 32:429–44.

Perrin, W.F. and Reilly, S.B. 1984. Reproductive parameters of dolphins and small whales of the family Delphinidae. *Rep. int. Whal. Commn* (special issue 6):97–133.

Perrin, W.F., Coe, J.M. and Zweifel, J.R. 1976. Growth and reproduction of the spotted porpoise, *Stenella attenuata*, in the offshore eastern tropical Pacific. *Fish. Bull., US* 74(2):229–69.

Perrin, W.F., Scott, M.D., Walker, G.J. and Cass, V.L. 1985. Review of geographical stocks of tropical dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern Pacific. NOAA Technical Report NMFS 28 (unpublished). 28pp.

Smith, T.D. 1979. Report of the status of porpoise stocks workshop (Aug. 27–73, La Jolla, California). Southwest Fisheries Center Admin. Rep. LJ-79–41 (unpublished).

Snedecor, G.W. and Cochran, W.G. 1973. *Statistical Methods*. Iowa State University Press, Iowa. 539pp.

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Ontogeny of the sodium pump in embryos of rockfish of the genus *Sebastes*

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Synopsis

The purpose of the present investigation was to determine at what stages of embryonic development the sodium pump (Na +, K + -activated ATP phosphohydrolase, EC 3.6.1.3) appears and whether the ontogeny of the sodium pump plays a role in the matrotrophic viviparity of *Sebastes*. Early larval stages (stages 1–14) had embryonic tissues nearly devoid of Na, K-ATPase activity. After epiboly, tissues from embryos taken from both species, *S. schlegeli* and *S. taczanowskii*, had significant levels of enzymatic activity coincident with the appearance of neuronal tissue in the head fold (stages 15–20). Maximal levels of specific activities of the enzyme were reached with the onset of the vascular circulation and the opening of the buccal cavity together with maturation of the midgut and hindgut regions of the intestinal tract (stages 26 and 28). Ouabain, a specific inhibitor of Na, K-ATPase, was used to measure survival of embryos placed in different seawater concentrations under in vitro conditions. The most sensitive stages to external ouabain were 26–30. These findings support the hypothesis that the intestinal tract is functional prior to gestation and could be transporting important nutritive material found in maternal ovarian fluid.

Introduction

Extracellular fluid regulation in adult and juvenile marine teleosts is dependent upon the osmoregulatory function of two extrarenal organs, the gill and the intestinal tract (Conte 1969, Hickman & Trump 1969, Kirsch et al. 1981, Alderdice 1988). The midgut region of the adult gastrointestinal tract counterbalances the integumental osmotic body water loss by permitting epithelial absorption of water and salt to occur after the fish begins drinking seawater. Simultaneously, the gill arch eliminates the excess salt from the ingested seawater by allowing chloride secretory cells of the gill filaments to secrete sodium chloride to the outside environment.

It is logical to assume that marine teleost larvae would regulate extracellular fluids by a similar style and employ extrarenal structures for achieving ionic and osmotic balance. Unfortunately, developmental patterns are not known for such extrarenal structures as the gut and gill, which show the functional interdependence between embryonic extrabranchial chloride cells and ionic function of the developing gill filaments (Alderdice 1988).

In transporting epithelia, such as that lining the midgut and gill filaments, the sodium pump [ouabain-sensitive, sodium and potassium ion coupled transport ATPase or Na, K-ATPase] represents the major driving force for the transepithelial transport of ions, organic molecules and water (Rossier et al. 1987). Fish gill and intestinal epithelia are rich in Na, K-ATPase enzymatic activity. In addition, the localization of Na, K-ATPase enzyme over the transporting epithelial cell surface is asymmetrically distributed and therefore gives the cell a functional polarity. In fact, the polarity of the epithelial sodium pump allows for vectorial transport of solute movement, which in turn controls volume and composition of extracellular fluids.

In oviparous species of teleost fishes, gametes are shed from the body, ovarian cavity or both, and fertilization together with embryogenesis occurs in the outside environment. In viviparous species, fertilization of gametes and development of the embryos and larvae occur within the ovary. Lecithotrophic viviparity is primarily dependent upon yolk material, stored in the egg following oogenesis, being sufficient to complete embryo development after fertilization. However, in matrotrophic viviparity, growth and development of the late embryonic stages are dependent upon maternal nutrition in addition to that stored in yolk platelets provided during oogenesis. Past research (Boehlert & Yoklavich 1984, Boehlert et al. 1986) on the reproductive mode exhibited by *Sebastes melanops* and *S. schlegeli* has given evidence that these species exhibit matrotrophic viviparity; females apparently provided nutrition during gestation of the embryo long after organogenesis but soon after the functional differentiation of the gut. This delayed gestation provides a time period allowing the maternal nutritional mechanism to act. In this case, the development of the intestinal transport epithelia along with the de novo synthesis of the sodium pumps probably is essential for nutritional uptake. For example, larvae at the late stages would initiate the drinking reflex and begin swallowing maternal ovarian fluid entering the buccal cavity. Following passage of this organically rich saline from the buccal cavity through the esophagus and stomach cavities, the fluid would enter into the lumen of the intestinal tract for assimilation. Upon reaching the midgut regions, the absorptive epithelium would transport water, ions and also nutrients, such as amino acids and proteins (Shimizu et al. 1991).

The purpose of this study was to determine at what stages of embryonic development the sodium pump appears and whether the ontogeny of the sodium pump plays a role in the matrotrophic viviparity of *Sebastes*.

Materials and methods

Experimental animals and developmental staging

White-edged rockfish, *S. taczanowskii*, were obtained by gill-netting or hook-line angling from the Usujiri shore near Hakodate, Hokkaido. Immediately after capture, fish were transported and placed in a 1-ton tank with flowing seawater and held until the start of the experiment. Kurosoi, *S. schlegeli*, were obtained from either captive brood stock at the Hokkaido Institute of Mariculture in Shikabe or were collected in Otobe in the Sea of Japan in May-June 1985. Fish were held in indoor tanks (1.8 × 1.8 × 1.1 m) with flowing seawater until the start of the experiment.

Pregnant females of *S. taczanowskii* were anesthetized with ethyl 4-aminobenzoate, then the ovaries were carefully dissected to allow removal of the developing embryos. Seven lots of 100 embryos were obtained from a pregnant female containing a single brood of synchronously developing embryos. In pregnant females of *S. schlegeli*, the embryos were removed by gently suction into a silicon tube inserted through the genital aperture. Classification of the embryonic stages used in the study followed the protocol described by Yamada & Kusakari (1991). Excess ovarian fluid was removed by blotting embryos with dry filter paper. Embryos were either frozen or used fresh for enzymatic analysis. Fresh embryos were placed in small (1 ml) glass homogenizers and homogenized in a sucrose-imidazole-EDTA (SIE) medium. Tissue homogenates were stored at − 40° C until chemical and enzymatic analyses could be performed.

Enzyme and ouabain-mortality analyses

Na + K-activated ATPase activity

The homogenizing medium (SIEs) used for *S. schlegeli* consisted of 0.25 M sucrose, 0.1 M imidazole buffer at pH 7.2 and 2 mM Na_2EDTA; the homogenizing medium (SIEt) used for *S. taczanowskii* consisted of 0.25 M sucrose, 0.02 M imidazole buffer at pH 6.8 and 6 mM Na_2EDTA. Fifty or one hundred embryos were added to 1.0 ml of SIE and homogenized for 1–2 min in a cold glass homogenizer. The homogenate was either stored in a freezer at − 40° C or used immediately for enzyme analysis.

The reaction mixture that gave optimal activity for *S. schlegeli* enzyme preparations consisted of 0.2 ml of salt solution (0.8 M NaCl, 0.2 M KCl), 0.2 ml of AMI solution (12.5 mM Na_2ATP, 25 mM $MgCl_2$, 250 mM imidazole, pH 7.2, with and without 12.5 mM ouabain) and 0.1 ml enzyme preparation. The reaction mixture was incubated at 37° C for 20 min and then stopped with 1.0 ml of 5 or 10% TCA reagent. Inorganic phosphate released from ATP was assayed by the method of Peterson et al. (1978). Protein was determined by the Peterson (1977) modification of Lowry et al. (1951) method by using serum albumin as the standard.

The reaction mixture that gave optimal activity for *S. taczanowskii* preparations consisted of 0.4 ml salt-substrate medium for *S. schlegeli* (337.5 mM NaCl, 162.5 mM KCl, 50 mM $MgCl_2$, 12.5 mM Na_2ATP, 250 mM imidazole, pH 7.0 with and without 2.5 mM ouabain) plus 0.1 ml of enzyme preparation. The reaction mixture was kept in an ice bath until the addition of enzyme, incubated at 37° C for 20 min and then stopped by adding 10 ml of 5% TCA reagent. Inorganic phosphate released from ATP was assayed by the method of Goldenberg & Fernandez (1966).

The specific activity of the sodium pump was determined as the difference between phosphate released in the absence and presence of ouabain. Activity was expressed as micromoles phosphate released per hour per mg protein or per 100 embryos.

Larval ouabain-mortality assays

Ouabain crystals (strophanthin G octahydrate, Sigma Chemical Co., St. Louis, MO) were added to each saline solution to a concentration of 1 mM. Sterilized seawater was used as the basic saline medium, and it was diluted with distilled water to 10, 33, 67% of full strength (100%) seawater. The associated osmolalities were 96, 304, 568 and 865 mosm · kg^{-1} respectively. Standard-sized petri dishes were filled with 20 ml of saline solution with and without ouabain. *Sebastes schlegeli* embryos at various stages of development were exposed in triplicate dishes; numbers of embryos per replicate ranged from 28 to 121. At select time intervals (24, 48 and 72 h), dead embryos were removed from the exposure dishes and counted.

Results

Embryonic Na, K-ATPase activity

The Na, K-ATPase activity in early developmental stages of both species was absent. However, as growth and development of the embryos proceeded, there occurred in the embryonic tissues an onset and elevation of Na, K-ATPase specific activities (Fig. 1). Apparently, all stages following epiboly have progressively higher enzyme levels. Unfortunately, fewer replicates were performed on *S. schlegeli* due to the lack of embryos, and the results of the enzymatic activities at the earliest stages were based upon only one aliquot of embryos. However, seven samples of embryos were available for enzymatic analysis at each stage of *S. taczanowskii* assayed. In *S. taczanowskii* it was found that among the embryo samples there appeared to be little enzymatic variability as shown by error bars. Thus, our interpretation of the developmental pattern for the Na, K-ATPase is based upon these data. For *S. taczanowskii* species there is an absence of Na, K-Atpase in the very early stages (stages 1–14) until well after epiboly. Following the appearance of the neuronal tissue in the head fold and the formation of the optic vesicle together with body somites (stages 15–20), the detectable levels

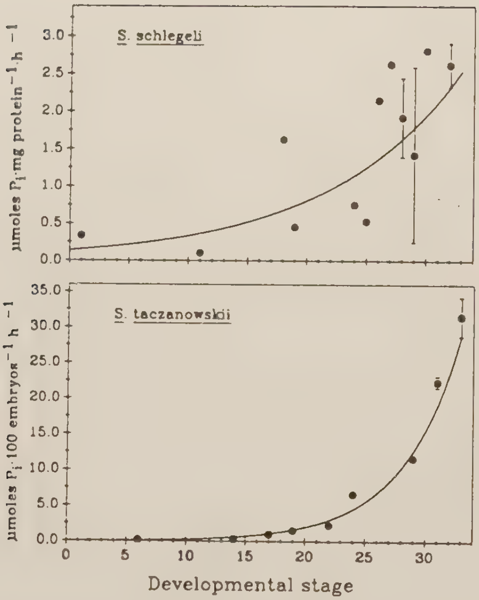

Fig. 1. Ontogeny of the sodium pump in two species of *Sebastes*. The difference in activities between absence and presence of ouabain are presented in two different ways for the different species. Data for *S. schlegeli* are fitted to the curve log (activity) = − 1.973 + 0.88 (stage), N = 12, r^2 = 0.583; all values are from a single determination except for stages 24 (2 determinations), 28 (3), 29 (2), and 32 (3). Data for *S. taczanowskii* are fitted to the curve log (activity) = − 3.441 + 0.206 (stage), N = 9, r^2 = 0.963; all values are the mean of seven replicates. Error bars represent 1 SD.

of enzyme activity increased substantially. However, the most dramatic increase in Na, K-ATPase specific activity occurred with the onset and establishment of the vascular circulation, the opening of the buccal cavity and the maturation of the midgut and hindgut regions of the intestinal tract (stages 26–28). These enzyme activity levels corresponded with the morphogenetic development of the post-abdominal body structures and remained relatively stable until hatching (stages 31–32), then increased dramatically. The high levels of enzyme activity in newborn larvae – somewhat higher than the hatching stages – might be related to the need to drink full-strength seawater.

Ouabain mortality during embryogenesis

The effect of ouabain, a specific inhibitor of Na, K-ATPase, on the survival of embryos placed in different external salines was measured. The ionic gradient and length of exposure impact the maintenance of osmotic equilibrium by the developing osmoregulatory organs at various stages of embryogenesis. Exposures to 10 and 100% seawater resulted in nearly 100% mortality of embryos at five different stages. Apparently 33 and 67% seawater constituted the more appropriate range for assaying embryonic osmoregulation and salt tolerance. Therefore, these salines were used to determine the effect of inhibiting the sodium pump with ouabain and its impact upon embryonic osmoregulation and salt regulation.

The earliest embryos tested (stages 1 and 24) were not affected by the presence or absence of 1 mM ouabain for exposure times of 24, 48 and 72 h at either 33 and 67% seawater. Longer exposure times of 48 and 72 h produced more variability among the control group mortalities, whereas the 24 h exposure time had relatively low mortalities at stages 24–30 as shown in Figure 2. In contrast, the sensitivity to external ouabain was observed to increase in stages 25, 28 and 30.

Discussion

Numerous studies on oviparous species of teleost fishes have shown that fertilized eggs and embryos can maintain osmotic gradients between the extracellular fluids and the external environment (Holliday & Jones 1965, 1967, Wiesbart 1968, Holliday 1969, Rudy & Potts 1969, Eddy 1974, Shen & Leatherland 1978, Tay & Garside 1978, Linden et al. 1979, Guggino 1980a, 1980b, Quast & Howe 1981). The major mechanism in the early life stages, such as from the zygote to the end of epiboly, transforms the perivitelline membrane from a semipermeable water barrier to one that is virtually impermeable (see review by Alderdice 1988). Called 'water hardening', this mechanism operates from the time of fertilization until the end of epiboly.

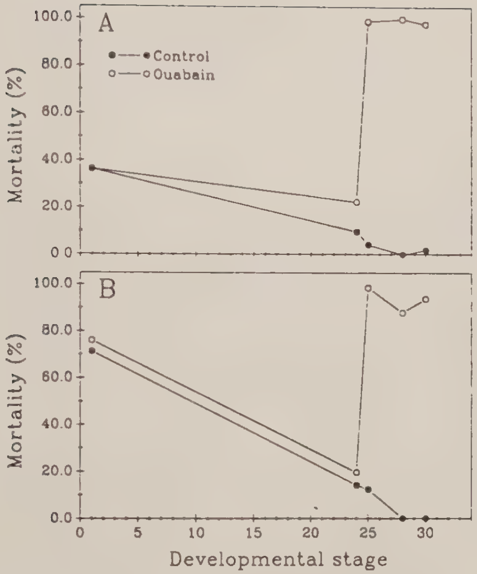

Fig. 2. Mortality rates in vitro for *Sebastes schlegeli* embryos at different developmental stages incubated in saline with and without 1 mM ouabain. Each point is the mean mortality rate of three replicates calculated after arcsine transformation: a – 304 mosm · kg^{-1} (33% seawater) saline, b – 568 mosm · kg^{-1} (67% seawater) saline.

From post-gastrulation to hatching, teleost fishes employ the mechanism of osmoregulation to compensate for fluid loss and utilize some type of osmoregulatory organ. Studies by Guggino (1980a, 1980b) have clearly shown that the osmotic water loss occurs along the embryonic integumentary surfaces. The fish embryo immediately initiates some type of drinking behavior to counterbalance the loss of fluid. In the killifish, *Fundulus heteroclitus*, the embryo has a measured drinking rate of 600 picoliters per mg protein per hour, as determined by the C^{14}-dextran method (Guggino 1980a, 1980b). Seawater does not enter through the mouth but rather through the branchial chambers that communicate anteriorly with the pharynx and posteriorly through pores connected to the perivitelline space. Excretion of excess salt is via ionic regulation that utilizes epithelial cells involved in active transport of ions. The site of extrusion of chloride ion has been identified as chloride cells in the epithelium lining the embryonic cavity and yolksac. After hatching occurs, the site of chloride secretion is mostly in the gill filaments. Unfortunately, measurement of the sodium pump enzyme has not been made in any of the larval stages. Hwang (1989) has reported the distribution and morphology of chloride cells in various teleost larvae.

Other oviparous species – in which the newly hatched embryos lack gill filaments and have the kidney represented only by the pronephric glomerulus and the gastrointestinal tract without either an oral or anal opening – have been shown to utilize other kinds of epithelial structures as pseudo-osmoregulatory organs. For instance, the skin reportedly is the major osmoregulatory organ for herring, *Clupea harengus* (Holliday & Jones 1965), plaice, *Pleuronectes platessa* (Holliday & Jones 1967), and sardine, *Sardinops sagax*, embryos (Lasker & Threadgold 1968), when placed in different levels of saline.

In contrast with the oviparous species, the number of studies on osmoregulation in embryos of viviparous species of teleosts is sparse (see review by Wourms et al. 1988). Since it has been shown by Veith (1979) that the follicular fluid is a benign osmotic environment in comparison with seawater, the protective function of the extraembryonic envelope, the chorion, may be unnecessary. Boehlert & Yoklavich (1984) have shown that the zona radiata was only 1.6% of the dry weight of the egg in *Sebastes melanops* and contrasts with the 15–33% found in oviparous marine teleosts (Blaxter & Hempel 1966, Robertson 1974). In *Sebastes*, the evidence obtained from the present study on the developmental staging of the membranous Na, K-ATPase suggests that osmoregulation occurs during the formation and opening of the mouth parts. The differentiation of the midgut is also accompanied by a dramatic increase in Na, K-ATPase specific activity, probably associated with the formation of microvilli and basolateral plications of the absorptive epithelium (Shimizu et al. 1991). The most perplexing observation from the present study is the finding that late stage embryos (stages 28–33) have the ability to be salt tolerant for short periods of time, but beyond 72 h, the osmoregulatory mechanism appears to become inefficient and salt tolerance cannot be sustained. One interpretation would be that the mechanism(s) controlling water and salt balance are not completely functional at these late stages. These findings are in agreement with the earlier work of Veith (1980), who compared the osmoregulatory ability of small and large embryos of the clinid, *Clinus superciliosus*. He showed that small embryos are capable of some degree of osmoregulation since they have good survival in 40–50% dilution of full-strength seawater. In 100% seawater, the small embryos exhibited high mortality, whereas the large embryos were fully functional and showed very few deaths. He concluded that water and ion fluxes across the embryonic exchange surfaces were too great in the small embryos to allow full regulation at the higher salinities. In the present study, it is clear that the sodium pump in *Sebastes* is playing an important role in osmoregulation. Although the ontogenetic pattern of the sodium pump in oviparous teleosts is poorly known, comparison with the viviparous *Sebastes* would be of interest since it would allow a greater degree of differentiating between the developmental role of the sodium pump in maternal nutrient uptake versus osmoregulation. Further research on this topic in *Sebastes* embryos should address the specific localization of the Na, K-ATPase in various transport type tissues.

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References cited

Alderdice, D.F. 1988. Osmotic and ionic regulation in teleost eggs and larvae. pp. 163–251. *In:* W.S. Hoar & D.J. Randall (ed.) Fish Physiology, Volume 11, Part A, Academic Press, San Diego.

Blaxter, J.H.S. & G. Hempel. 1966. Utilization of yolk by herring larvae. J. Mar. Biol. Assoc. U.K. 46: 219–234.

Boehlert, G.W., M. Kusakari, M. Shimizu & J. Yamada. 1986. Energetics during embryonic development in kurosoi, *Sebastes schlegeli* Hilgendorf. J. Exp. Mar. Biol. Ecol. 101: 239–256.

Boehlert, G.W. & M.M. Yoklavich. 1984. Reproduction, embryonic energetics, and the maternal-fetal relationship in the viviparous genus *Sebastes* (Pisces: Scorpaenidae). Biol. Bull. 167: 354–370.

Conte, F.P. 1969. Salt secretion. pp. 241–283. *In:* W.S. Hoar & D.J. Randall (ed.) Fish Physiology, Volume 1, Academic Press, New York.

Eddy, R.B. 1974. Osmotic properties of the periviteline fluid and some properties of the chorion of Atlantic salmon eggs *(Salmo salar)*. J. Zool. London 174: 237–243.

Goldenberg, H. & A. Fernandez. 1966. Simplified method for the estimation of inorganic phosphorous in body fluids. Clin. Chem. 12: 871–882.

Guggino, W.B. 1980a. Salt balance in embryos of *Fundulus heteroclitus* and *F. bermudae* adapted to sea water. Amer. J. Physiol. 238: R42–R49.

Guggino, W.B. 1980b. Water balance in embryos of *Fundulus heteroclitus* and *F. bermudae* adapted to sea water. Amer. J. Physiol. 238: R36–R41.

Hickman, C.P. & B.F. Trump. 1969. The kidney. pp. 91–227. *In:* W.S. Hoar & D.J. Randall (ed.) Fish Physiology, Volume 1, Academic Press, New York.

Holliday, F.G.T. 1969. The effects of salinity on the eggs and larvae of teleosts. pp. 293–309. *In:* W.S. Hoar & D.J. Randall (ed.) Fish Physiology, Volume 1,Academic Press, New York.

Holliday, F.G.T. & M.P. Jones. 1965. Osmotic regulation in the embryo of the herring *(Clupea harengus)*. J. Mar. Biol. Assoc. U.K. 45: 305–311.

Holliday, F.G.T. & M.P. Jones. 1967. Some effects of salinity on the developing eggs and larvae of the plaice *(Pleuronectes platessa)*. J. Mar. Biol. Assoc. U.K. 47: 39–48.

Hwang, P.P. 1989. Distribution of chloride cells in teleost larvae. J. Morphology 200: 1–8.

Kirsch, R., R. Meens & M.F. Meister. 1981. Osmoregulation in marine teleosts: Role of gills and digestive tube. Bull. Soc. Zool. France 106: 31–36.

Lasker, R. & L.T. Threadgold. 1968. 'Chloride cells' in the skin of the larval sardine. Exptl. Cell Res. 52: 582–590.

Linden, O., J.R. Sharp, R. Loughlin & J.M. Neff. 1979. Interactive effects of salinity, temperature and chronic exposure to oil on the survival and developmental rate of embryos of the estuarine killifish *Fundulus heteroclitus*. Mar. Biol. 51: 93–100.

Lowry, O.H., N.J. Rosebrough, A.L. Farr & R.J. Randall. 1951. Protein measurement with the Folin phenol reagent. J. Biol. Chem. 193: 265–275.

Peterson, G.L. 1977. A simplification of the protein assay method of Lowry et al. which is more generally applicable. Anal. Biochem. 83: 346–356.

Peterson, G.L., R.D. Ewing, S.R. Hootman & F.P. Conte. 1978. Large scale purification and molecular and kinetic properties of the (Na + K)-activated adenosine triphosphatase from *Artemia salina* nauplii. J. Biol. Chem. 253: 4762–4770.

Quast, W.D. & N.R. Howe. 1981. The osmotic role of the brood pouch in the pipefish *Syngnathus scovelli*. Comp. Biochem. Physiol. 67A: 675–678.

Robertson, D.A. 1974. Developmental energetics of southern pigfish (Teleostei: Congriopodidae). N. Z. J. Mar. Freshwater Res. 8: 611–620.

Rossier, B.C., K. Geering & J.P. Kraehenbuhl. 1987. Regulation of the sodium pump: how and why? Trends Biochem. Sci. 12: 483–487.

Rudy, P.P. & W.T.W. Potts. 1969. Sodium balance in the eggs of the Atlantic salmon, *Salmo salar*. J. Exp. Biol. 50: 234–246.

Shen, A.C.Y. & J.F. Leatherland. .1978. Effect of ambient salinity on ionic regulation and osmotic regulation of eggs, larvae and alevins of rainbow trout *(Salmo gairdneri)*. Can. J. Zool. 56: 571–577.

Shimizu, M., M. Kusakari, M.M. Yoklavich, G.W. Boehlert & J. Yamada. 1991. Ultrastructure of the epidermis and digestive tract in *Sebastes* embryos, with special reference to the uptake of exogenous nutrients. Env. Biol. Fish. 30: 155–163

Tay, K.L. & E.T. Garside. 1978. Compensatory embryogenic responses in osmoregulatory structures of mummichog *Fundulus heteroclitus* L. incubated at constant temperature and various constant levels of salinity. Can. J. Zool. 56: 613–618

Veith, W.J. 1979. The chemical composition of the follicular fluid of the viviparous teleost *Clinus superciliosus*. Comp. Biochem. Physiol. 63A: 37–40.

Veith, W.J. 1980. Viviparity and embryonic adaptations in the teleost *Clinus superciliosus*. Can. J. Zool. 58: 1–12.

Weisbart, M. 1968. Osmotic and ionic regulation in embryos, alevin and the fry of five species of Pacific salmon. Can. J. Zool. 46: 385–397.

Wourms, J.P., B.D. Grove & J. Lombardi. 1988. The maternal-embryonic relationship in viviparous fishes. pp. 1–134. *In:* W.S. Hoar & D.J. Randall (ed.) Fish Physiology, Volume 11, Part B, Academic Press, San Diego.

Yamada, J. & M. Kusakari. 1991. Staging and the time course of embryonic development in kurosoi, *Sebastes schlegeli*. Env. Biol. Fish. 30: 103–110.

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CARETTACOLA HAWAIIENSIS N. SP. (TREMATODA: SPIRORCHIDAE) FROM THE GREEN TURTLE, *CHELONIA MYDAS*, IN HAWAII

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ABSTRACT: *Carettacola hawaiiensis* n. sp. (Trematoda: Spirorchidae) is described from the hepatic vessels of the green turtle, *Chelonia mydas* (L.), in Hawaii. The new species differs from any previously described species of *Carettacola* in size, placement of vitellaria, and shape and placement of Laurer's canal. The genus *Haemoxenicon* Martin and Bamberger, 1952, becomes a synonym of *Carettacola* Manter and Larson, 1950. *Haemoxenicon stunkardi* Martin and Bamberger, 1952, is transferred to the genus *Carettacola* Manter and Larson, 1950, and becomes *Carettacola stunkardi* n. comb. An emended generic diagnosis for *Carettacola* is given along with a key to the species.

From 1986 to 1988, 10 green sea turtles (*Chelonia mydas* (L.)) were found stranded on the islands of Lanai, Maui, and Oahu in Hawaii. The turtles were covered with neoplasms identified as fibropapillomas. These growths on turtles can result in reduced vision, disorientation, blindness, and physical obstruction to normal swimming and feeding. Upon determination that the turtles would not survive, they were killed and examined for parasites. Two turtles, 1 from Kaneohe Bay, Oahu, and 1 from Kahului Bay, Maui, were infected with an undescribed species of the genus *Carettacola* Manter and Larson, 1950.

MATERIALS AND METHODS

A thorough examination for parasites was carried out on the lungs, liver, heart, major vessels, stomach, intestine, and bladder. Worms were placed in tap water and refrigerated overnight for egg expulsion, fixed in alcohol–formalin–acetic acid (AFA) for 2 days, and then transferred to 70% ethyl alcohol for storage. Whole mounts were stained in Semichon's acetocarmine, dehydrated in a graded ethanol series, and mounted in Canada balsam. Drawings were made with the aid of a drawing tube. Measurements are in micrometers unless otherwise indicated, with range followed by mean in parentheses. Representative specimens have been deposited in the United States National Museum (USNM) Helminthological Collection, Beltsville, Maryland, and the Harold W. Manter Laboratory (HWML), Division of Parasitology, University of Nebraska State Museum, Lincoln, Nebraska. The balance of the specimens are deposited in the Institute of Parasitology, California State University, Long Beach, California.

DESCRIPTION

Carettacola hawaiiensis n. sp.
(Figs. 1–4)

Diagnosis (based upon measurements of 8 whole specimens): Spirorchidae Stunkard, 1921; Carettacolinae Yamaguti, 1958. Body elongate, 5.0–7.7 mm (6.5) long, maximum width 0.210–0.380 mm (0.310) at midbody. Oral sucker terminal, 105–178 (160) long by 84–131 (112) wide with short spines around perimeter. Esophagus tubular, 0.92–1.16 mm (1.01) long, posterior third becoming flask-shaped at cecal bifurcation. Gland cells occur along esophagus particularly at narrow anterior portion of flask-shaped enlargement. Intestinal ceca slightly sinuous, terminating near anterior ends of forks of Y-shaped excretory vesicle. Acetabulum approximately 22% of body length from anterior end, 200–280 (230) in diameter, immediately posterior to intestinal bifurcation, weakly muscular, protrusible, and ringed with small spines. Testes number 34–48 (40), 156–278 (205) by 94–134 (121) wide, in irregular linear series filling most of posterior intercecal field. Genital pore ventrosinistral, approximately 32% of body length from anterior end. External seminal vesicle saccate, 101–161 (125) long by 88–131 (103) wide, anterior to cirrus sac, filling intercecal area between acetabulum and cirrus sac. Cirrus sac large, 287–337 (307) long by 104–125 (121) wide, partly an-

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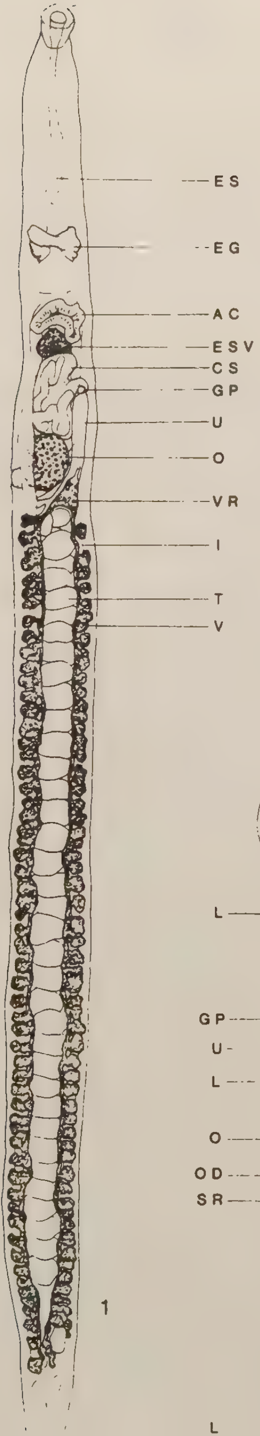
FIGURES 1–9. *Carettacola hawaiiensis* n. sp. from the green turtle in Hawaii, *Carettacola bipora*, and *Carettacola stunkardi* n. comb. with diagrams of female reproductive organs from each. 1-4. *Carettacola hawaiiensis* n. sp. 1. Entire worm (ventral view). 2. Lateral view of acetabulum and cirrus. 3. Vitellaria formed around ventral surface of ceca. 4. Egg. 5. *Carettacola bipora* (ventral view). 6. *Carettacola stunkardi* n. comb. (ventral view). 7-9. Female reproductive organs of *Carettacola bipora*, *Carettacola hawaiiensis*, and *Carettacola stunkardi*. 7. *Carettacola bipora*. 8. *Carettacola hawaiiensis*. 9. *Carettacola stunkardi*. Scale used for all figures except reproductive organs (7, 8, 9). ES, esophagus; EG, esophageal gland; AC, acetabulum; ESV, external seminal vesicle; CS, cirrus sac; GP, genital pore; U, uterus; O, ovary; OD, oviduct; VR, vitelline reservoir; I, intestinal cecum; L, Laurer's canal; SR, seminal receptacle; T, testis; V, vitellaria.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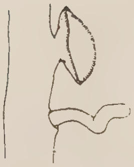

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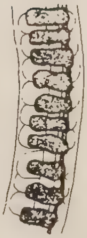

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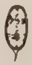

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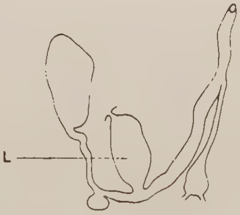

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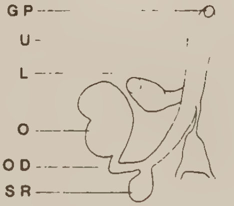

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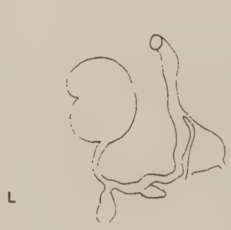

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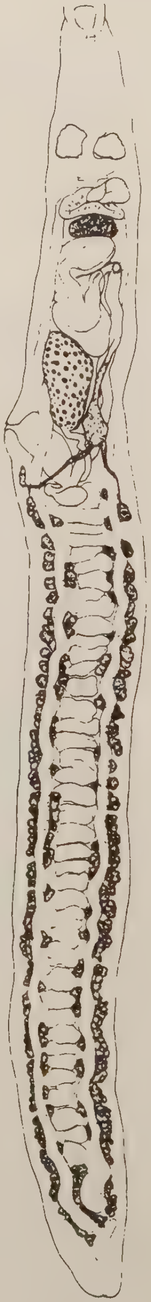

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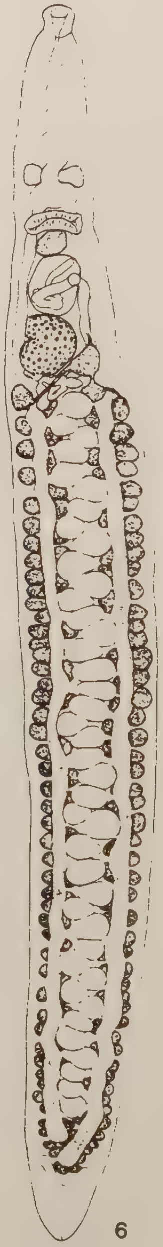

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terior but mostly posterior to common genital pore, partly overlapping ovary, containing tubular seminal vesicle, numerous large prostatic cells, and long aspinous cirrus.

Ovary reniform, 220–280 (250) long by 150–220 (190) wide, intercecal, about ⅓ body length from anterior end; oviduct extends posteriorly then turns sinistral and is joined by small, spherical seminal receptacle. Oviduct extends to edge of cecum, bends anteriad, and enters uterus near common vitelline duct. The uterus extends anteriorly where it is joined by Laurer's canal. Laurer's canal opens dorsolaterally through marginal pore, opposite posterior end of ovary. Vitelline follicles large, primarily extracecal, roughly C-shaped, ventral to ceca; measuring 173–236 (203) long by 89–131 (106) wide; extending from level of anterior testis to ends of ceca. Uterus short, in several specimens contained large single egg. Egg, 174–184 (179) long by 63–84 (74) wide, with posterior spine (21–36 long). Mehlis' gland not observed.

Taxonomic summary

Type host: *Chelonia mydas* (L.).

Type locality: Kaneohe Bay, Oahu, Hawaii.

Additional localilty: Kahului Bay, Maui, Hawaii.

Site: Hepatic vessels.

Specimens deposited: Holotype USNM Helminthological Collection no. 81897, paratypes, USNM Helminthological Collection no. 81897 and HWML 33435.

Etymology: The species is named after state in which it was found.

Remarks

Carettacola hawaiiensis closely resembles both *Carettacola bipora* Manter and Larson, 1950, from the loggerhead turtle *Caretta caretta* (L.) collected at Tortugas, Florida, and *Haemoxenicon stunkardi* Martin and Bamberger, 1952, from the green turtle (*C. mydas*) collected off Baja, California. However, in addition to differing from both in total length and width, *C. hawaiiensis* also differs by having vitelline follicles encircling the ceca ventrally, large vaginalike Laurer's canal, and Laurer's canal joining to the uterus rather than oviduct. The acetabulum of *C. hawaiiensis* does not have a center membranous flap as does *C. bipora* and the Laurer's canal "vaginal walls" of *C. hawaiiensis* are not thick and muscular as found in *C. bipora.* The egg of *C. hawaiiensis* is larger than that of either *C. bipora* or *H. stunkardi.*

During this study the holotypes of *C. bipora* (USNM Helm. Coll. no. 37177) and *H. stunkardi* (Hancock Parasit. Coll. no. 499) were examined. *Haemoxenicon stunkardi* could not be separated from the genus *Carettacola* by criteria given in the original description. *Carettacola bipora* has a common genital pore and not separate male and female pores as originally described. Also, *H. stunkardi* has a flask-shaped "stomach" area just anterior to the cecal bifurcation as does *C. bipora* and *C. hawaiiensis.* The "minute dorsal Laurer's pore" described for *Haemoxenicon* by Martin and Bamberger (1952) appears to be a reduced version of the same structure found in both *C. bipora* and *C. hawaiiensis.* These findings indicate that *H. stunkardi* should be placed in the genus *Carettacola* and the generic diagnosis emended to include *Haemoxenicon* Martin and Bamberger, 1952. *Haemoxenicon stunkardi* is transferred to *Carettacola* and becomes *Carettacola stunkardi* n. comb. *Haemoxenicon* is reduced to a junior synonym of *Carettacola.* An emended generic diagnosis of *Carettacola* follows.

Carettacola Manter and Larson, 1950

Emended generic diagnosis: Spirorchidae, Carettacolinae. Body slender, almost uniform in width. Oral sucker terminal, esophagus long, ceca terminating near posterior extremity. Acetabulum located immediately posterior to intestinal bifurcation, membranous, variable shape. Testes numerous, arranged in linear series, filling most of posterior intercecal field; external seminal vesicle, filling intercecal area between acetabulum and cirrus pouch. Cirrus pouch large, postacetabular, containing tubular seminal vesicle, numerous prostate cells. Cirrus armed or unarmed. Genital pore ventrosinistral to cirrus pouch, posterior to acetabulum, preovarian. Ovary oval to reniform, intercecal, immediately behind cirrus pouch. Receptaculum seminis small. Laurer's canal present behind or overlapping ovary, may or may not be expanded behind pore with muscular walls. Vitelline follicles extending around ceca from level of anterior testis to cecal ends. Uterus short, containing a single egg with polar filament. Excretory vesicle Y-shaped, with terminal pore. Parasites of marine turtles.

Type species: *Carettacola bipora* Manter and Larson, 1950.

KEY TO SPECIES OF *CARETTACOLA*

1a. Vitellaria formed around ventral surface of cecal branches . . . . *C. hawaiiensis*
1b. Vitellaria formed around dorsal surface of cecal branches 2
2a. Laurer's canal expanded behind lateral pore-forming muscular sac . . . . *C. bipora*
2b. Laurer's canal with only minute pore opening on dorsal surface without muscular sac . . . . *C. stunkardi*

DISCUSSION

Glazebrook et al. (1989) listed the most common sites for cardiovascular flukes in marine turtles as the heart, followed by visceral vessels. *Carettacola bipora* was found in intestinal washings of the loggerhead turtle, but the worms were believed to have originated from a nearby blood vessel (Manter and Larson, 1950). Glazebrook et al. (1989) listed *C. bipora* from "abdominal blood vessel." *Haemoxenicon stunkardi* and *Haemoxenicon chelonenecon* Martin and Bamberger, 1952, were found in mesenteric veins of *C. mydas. Haemoxenicon chelonenecon* subsequently has been synonymized with *H. stunkardi* by Caballero et al. (1955). *Carettacola hawaiiensis* is the first trematode found in the hepatic vessels of a marine turtle. The occurrence of these 3 worms in the vascular system of organs other than the heart and associated major vessels sets them apart from other sea turtle spirorchids.

When the 3 species are compared the configuration of the arrangement of internal structures is nearly identical (Figs. 1, 5, 6). The occurrence of a well developed Laurer's canal in all 3 worms (Figs. 7–9) also differentiates these parasites from other known spirorchids infecting marine turtles. The true uterus is very short in all 3 species, with the Laurer's canal being an offshoot of the uterine region in *C. hawaiiensis* rather than the oötype region (near the seminal receptacle) as in *C. bipora* and *C. stunkardi.* Another unique feature shared by only these 3 spirorchid worms is the C-shaped vitelline follicles that encircle the cecal branches, *C. hawaiiensis* ventrally (Fig. 3) and *C. bipora* and *C. stunkardi* dorsally (Figs. 5, 6).

ACKNOWLEDGMENTS

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LITERATURE CITED

Caballero, y C. E., M. C. Zerecero y D., and R. G. Grocott. 1955. Helmintos de la República de Panamá. XV. Tremátodos de *Chelone mydas* (L.), tortuga marina comestible del Océano Pacífica del Norte. 2a parte. Anales del Instituto de Biología, México **26:** 149–191.

Glazebrook, J. S., R. S. F. Campbell, and D. Blair. 1989. Studies on cardiovascular fluke (Digenea: Spirorchiidae) infections in sea turtles from the Great Barrier Reef, Queensland, Australia. Journal of Comparative Pathology **101:** 231–250.

Manter, H. W., and M. I. Larson. 1950. Two new blood flukes from a marine turtle, *Caretta caretta.* Journal of Parasitology **36:** 595–599.

Martin, W. E., and J. W. Bamberger. 1952. New blood flukes (Trematoda: Spirorchidae) from the marine turtle, *Chelonia mydas* (L.). Journal of Parasitology **38:** 105–110.

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'FIERY BODIES' – ARE PYROSOMAS AN IMPORTANT COMPONENT OF THE DIET OF LEATHERBACK TURTLES?

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INTRODUCTION

Until the careful work of Bleakney (1965) and Brongersma (1969) the diet of Leatherback Turtles (*Dermochelys coriacea* (L.)) was obscure; they were variously thought to be herbivores, omnivores, predators on fish or crustacea, or specialist squid-eaters. Bleakney and Brongersma (*op. cit.*) established from analysis of stomach contents that the diet of Leatherbacks caught or stranded in coastal waters of North America and Europe was made up of jellyfish (medusae) and associated animals (such as hyperiid amphipods). Direct observations of jellyfish-eating have since been made, particularly around the Irish, Welsh and French coasts, where Leatherbacks are regularly observed consuming large medusae in August and September. The concept that Leatherbacks are specialized medusivores has been widely accepted, and Holland *et al* (1990) recently demonstrated that the fatty acid signature of *Dermochelys* blubber is compatible with a jellyfish diet. However, in this paper we demonstrate that another group of animals, the pyrosomas ('fiery bodies' so named by virtue of their bright bioluminescence) may also be important dietary items in some circumstances.

Three major groups of gelatinous, pelagic marine animals are known; the cnidarians (medusae and siphonophores), the ctenophores (combjellies) and the tunicates. As far as Leatherback diet is concerned, most observers have concentrated upon the carnivorous cnidarians, particularly the swarms of jellyfish which are seen in temperate and tropical coastal waters, and on which *Dermochelys* is known to feed. However, in the waters above the continental slope, and in the open ocean, tunicates (which are predominantly herbivorous) are at least as common. Two groups of tunicates, the pyrosomas and the salps, attain sizes great enough to make them potential prey for adult Leatherbacks; they also occur in dense swarms in areas of upwelling where primary production is high.

Pyrosomas are colonies of tunicate zooids embedded in the walls of gelatinous tubes which are closed at one end and open at the other (Berrill, 1950). Each zooid draws water individually from the surrounding sea (through the branchial siphon), but all zooids exhale through the atrial siphons into the interior of the tube, thereby producing jet propulsion via its open end (guarded by a diaphragm). This propulsion is powerful enough to permit extensive vertical migrations. During the day pyrosomas are often found at depths of 500-800 m (within the known diving capability of Leatherbacks – Eckert *et al,* 1986), but migrate upwards at night, often into surface waters (Marshall, 1979). Pyrosomas are brightly luminescent, producing blue-green light (482m) with a secondary green peak (525m) according to Boden and Kampa (1964). Pyrosoma light displays last for many seconds, even minutes. Pyrosomas range in size from a few cm to more than 4 m according to Marshall. Specimens 0.2-0.5 m are very common in summer. They can be soft in texture, but most of the larger pyrosomas are rather cartilagenous/leathery despite their gelatinous nature.

Salps are barrel-shaped tunicates. Some are solitary and can be up to 0.2 m in length; others occur in chain-like colonies (up to 2 m length), whose jet propulsion (muscular in this case) is synchronized. Like pyrosomas, salps are bioluminescent and distributed widely through the top 800 m of the water column. Salps have a very high water content (98.3% according to

Riley and Gorgy, 1948), which would superficially make them rather meagre food resources. However, Kashkina (1986) notes that salps (and by implication other tunicates including pyrosomas, since all share a common feeding mechanism) have a stomach (the 'nucleus') full of compacted phytoplankton, detritus and microzooplankton. He also lists a wide variety of fish which feed upon salps and pyrosomas, often as major items of diet. Fish living in upwelling areas, near sea mounts and on the continental slope, seem particularly dependent upon pelagic tunicates.

Davenport (1988) suggested that the Leatherback might forage upon pyrosomas during deep dives; he thought that the colonies might be located by their bioluminescence. Direct evidence to support this hypothesis was lacking, although Marshall (1979) stated that sea turtles (species unspecified), together with sea birds and fish, had been observed to feed on glowing pelagic tunicates at the sea surface at night.

This paper lists records of occurence of pyrosomas in the gut of Leatherback Turtles and also presents details of the food value of pyrosomas, including an analysis of their fatty acid composition.

ANALYTICAL METHODS

Large numbers of *Pyrosoma atlantica* were collected on Cruise 195 of R.V. *Discovery* off the west African coast. Collection, by midwater net (8 m^2 mouth), took place in September 1990 in a large sea area (roughly 17-21 N; 19-25 W) at depths between 500 and 1000m. The colonies were washed briefly in fresh water, dried in absorbant paper, placed in polythene bags and frozen at -20°C. On return to a shore facility four colonies were analyzed in the following manner. The colonies were each weighed, dried in a freeze-drier and reweighed. Duplicate pieces of dried material were taken from each colony, weighed, ashed in a furnace at 570°C, allowed to cool in a desiccator and reweighed. Other samples of dried material were analyzed for protein content by a micro-Kjeldahl technique, for caloric content by wet oxidation (using an appropriate correction for unreacted protein) and for lipid content by solvent extraction and subsequent gravimetric measurement. Samples of pyrosoma lipid were further analyzed for fatty acid composition by gas chromatography.

RESULTS

1. RECORDS OF LEATHERBACKS FORAGING ON *PYROSOMA* IN THE INSULAR NORTH PACIFIC OCEAN

a) Iverson & Yoshida (1956) plus personal communication to G. Balazs by Tom Hida.

Date and Location: May 21st, 1954, 5 57.5' N, 161 11.0' W; on the high seas, 100 km east of Palmyra Island.

A Leatherback of greater than or equal to 91 cm carapace length was tangled in longline fishing gear. The "gastrointestinal tract found to be filled completely through with Pyrosoma".

b) by Jones & Shomura (1970).

Date and Location: July 21st, 1969. 3 30' N, 145 0' W; on the high seas.

106 cm carapace length Leatherback hooked alive in the "shoulder" in longline fishing gear. Report states "stomach contents of the Leatherback turtle were examined and consisted entirely of *Pyrosoma* colonies".

c) Balazs & Gilmartin (unpublished data)

Date and Location: March 24th, 1982. 21 10' N, 157 43' W; Waimanalo Bay, Oahu, Hawaiian Islands.

137 cm carapace length Leatherback stranded ashore alive, with all four flippers recently amputated, presumably by sharks. "When necropsied, the gastrointestinal contents were found to consist of liquid, one whole *Pyrosoma* and several *Pyrosoma* fragments, and three pieces of cellophane".

From these records it seems that pyrosomas are found in the gut of turtles foraging in oceanic waters (rather than on the continental shelf). Pyrosomas may also be identifiable throughout the gut (Iverson & Yoshida, 1956).

2. RECORDS OF LEATHERBACKS FORAGING ON *PYROSOMA* IN THE SOUTH PACIFIC OCEAN

Some years ago one of the authors (JD) saw a mounted Leatherback in the Dunedin Museum, South Island, New Zealand. The associated label stated that the turtle had been caught in oceanic waters north of North Island, New Zealand; it had pyrosomas in the stomach.

3. RECORDS OF LEATHERBACKS FORAGING ON PYROSOMA IN THE MEDITERRANEAN

Location: Gulf of Genoa, northern Mediterranean.

Capra (1949) found "remains of six specimens of a *Pyrosoma* species in the intestine of a Leathery Turtle, which had become entangled in nets off the Punta della Chiappa. One *Pyrosoma* specimen had a length of 50 cm, but it was much lacerated; the others measured 15 to 20 cm".

4. ANALYSIS OF *PYROSOMA ATLANTICA*

TABLE 1

Water and organic content of *Pyrosoma atlantica*

Colony no.	Wet wt (g)	dry wt (g)	dry wt as % wet wt	water as %wet wt
1	52.57	2.87	5.46	94.54
2	46.92	2.27	4.84	95.16
3	21.33	1.57	7.36	92.64
4	16.49	1.25	7.58	92.42
		mean	6.31	93.69
		SD	1.37	1.37

Colony no.	Ash as % dry wt	Organic content as % dry wt	Organic content as % wet wt
1	65.7	34.3	1.82
1	67.5	32.5	
2	62.4	37.6	1.80
2	63.4	36.6	
3	60.4	39.6	3.02
3	57.4	42.6	
4	55.3	44.7	3.41
4	54.7	45.3	
mean	60.8	39.2	2.51
SD	4.7	4.7	0.83

Table 1 shows the water and organic content of *Pyrosoma atlantica*. The tunicate colonies have a water content of about 94%; some 39% of the dried material is organic in nature, 61% inorganic. In consequence, only 2.5% of the weight of live colonies is composed or organic material. The water contents are similar to those of cnidarians (medusae and siphonophores) (Marshall, 1979), but pyrosomas are less watery than salps. The organic content of pyrosomas is close to the upper limit of the range (0.5-2.5%) given for medusae by Teissier (1926).

TABLE 2

Biochemical composition of *Pyrosoma atlantica*

Colony no.	mean protein content (g protein/mg dry wt)	mean lipid content (g lipid/mg dry wt)	mean calorific content (cals/mg dry wt)
1	90.6	9.0	0.78
2	110.4	–	1.04
3	91.3	14.0	1.26
4	134.4	–	1.66
mean	106.7	11.5	1.18

Table 2 shows the biochemical makeup of dried *Pyrosoma*. Taken with the organic content data shown in Table 1, this means that about 27% of the organic material in pyrosomas is composed of protein, 3% of lipid and (by difference) 70% of carbohydrate (presumably mainly mucopolysaccharides to give the gelatinous structure). Both protein and lipid values are low by the standards of marine animals such as fish and mollluscs which might be expected to have protein and lipid contents of about 45% and 8% respectively). However, the values are not dissimilar from those reported from cnidarians. The caloric value (about 3 cals/mg dry organic wt) is also very low, lower than all of the organisms listed by Crisp (1971).

TABLE 3

Fatty acid composition (%) of two colonies of *Pyrosoma atlantica*. Data for Leatherback turtle carapace blubber (neutral fraction) and for jellyfish (*Rhizostoma, Cyanea*) are given for comparison; they are taken from Holland, Davenport & East (1990)

Fatty acid	*Pyrosoma* Colony no. 1	*Pyrosoma* Colony no. 2	*Dermochelys*	*Rhizostoma*	*Cyanea*
A. Saturated					
12:0	–	–	5.6	0.3	0.1
13:0	–	–	tr	0.6	0.3
14:0	14.8	12.5	11.5	5,1	3.5
15:0	–	–	0.6	2.0	1.3
16:0	36.5	25.9	15.9	27.3	19.0
17:0	–	–	0.8	2.3	1.0
18:0	3.3	1.9	7.5	21.7	12.0
19:0	–	–	0.3	0.5	1.2
20:0	–	–	0.3	tr	1.8
B. Monounsaturated					
16:1 7	–	–	9.5	3.8	4.7
16:1 9	6.1	5.9	–	–	–
18:1 9	10.1	12.2	25.4	6.8	5.5
18:1 7	1.6	2.2	4,9	3.5	3,1
20:1 9	–	0.4	2.2	0.8	3.4
22:1 11	2.8	1.3	–	–	2.5
C. Polyunsaturated					
18:2 6	1.9	3.2	1.5	1.6	0.4
18:3 3	1.3	1.2	0.6	1.6	0.4
18:4 3	2.3	3.1	0.4	2.8	0.6
20:8 6	2.3	3.5	2.1	2.8	8.7
20:5 3	4.2	5.9	4.5	9.7	13.8
22:5 3	1.2	0.7	1.8	1.3	3.2
22:6 6	11.7	20.3	4.6	5.3	12.1

tr = trace quantities; – = not detected

Table 3 shows the fatty acid composition of *Pyrosoma*. As with jellyfish, pyrosoma lipids are rich in the saturated fatty acids 14:0 and 16:0, the monounsaturated fatty acid 18:1 9 and the polyunsaturated fatty acids 20:5 3 and 22:6 6. There are also reasonable levels of arachidonic acid (20:4 6). These data, combined with those for Leatherback blubber (Holand *et al*, 1990) are consistent with the concept of a phytoplankton – pyrosomas – Leatherback food chain (assuming that Leatherbacks accumulate fatty acids directly from the diet, rather than synthesizing them *de novo*).

DISCUSSION

The records drawn together here, plus the results of the analysis of *Pyrosoma atlantica* indicate that pyrosomas are important items of the Leatherback diet and have a composition quite similar to medusae. It is tempting to speculate that pyrosomas are more important to Leatherbacks swimming in mid ocean than they are to turtles foraging in coastal water, but more data are needed to clarify this point, particularly as Capra (1949) reported pyrosomas from the gut of a turtle swimming in the relatively shallow Gulf of Genoa. As Den Hartog & Van Nierop (1984) point out, the whole concept of medusivory stems from analysis of stomach contents of a relatively small number of Leatherbacks stranded or observed in northern temperate waters. Given that Leatherbacks are also known to eat the Portuguese Man O'War (a siphonophore – *Physalia*) (Bacon, 1970) and inappropriate floating objects such as plastic bags and polystyrene, it seems likely that *Dermochelys* is an opportunist rather than a specialist predator on fairly large, slow moving gelatinous prey.

A longstanding problem in considerations of the nutrition of Leatherbacks is that their food is very watery and the organic component is made up largely of mucopolysaccharides. This is true whether the diet is predominantly of medusae (the conventional view) or is made up to some extent of tunicates (this paper). Such a poor quality diet means that adult Leatherbacks must consume very large quantities of food (perhaps 20-30% body weight per day, rather than the 3-5% of Green and Loggerhead turtles). Duron (1978) reported that large Leatherbacks foraging on the medusa *Rhizostoma* off the French coast each ate about 200 kg of jellyfish per day. However, there are still problems in assimilating protein and lipids from jellyfish or tunicates, against a background of essentially indigestible mucopolysaccharide. Kashkina (1986) has raised an interesting possibility; that salp-eating fish probably only assimilate energy-rich material from the salp stomach, and pass the bulk of the gelatinous tunic through the gut without digesting it. This reasoning could equally be applied to medusae, which will contain partly digested food within the stomach and radial canals, and also have concentrations of organic material in the gonads during the breeding season. If a Leatherback turtle could gain access to the more 'valuable' parts of prey, it would not need to waste time and energy in digesting the tunic of tunicates and the mesogloea of coelenterates. Leatherback turtles cannot chew food items, which appear to be swallowed whole, or at least in large chunks. However, the entire oesophagus of *Dermochelys*, which may be more than 2 m long in large specimens, is lined with hundreds of long, semirigid cornified conical processes; the oesophagus is also very muscular, probably allowing the oesophageal contents to be squeezed by peristaltic waves. If cnidarians and salps were effectively shredded, the tubular conformation of pyrosoma colonies presents a relatively large surface area to the surrounding medium. At least one of the records presented here (Iverson & Hoshida, 1956; Hida, pers. comm.) indicates that some pyrosomas are still identifiable in the hind gut – supporting the idea of the tough test passing through the digestive tract relatively unchanged.

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REFERENCES

Bacon, P.R. (1970). Studies on the leatherback turtle *Dermochelys coriacea* (L.), in Trinidad, West Indies. *Biological Conservation*, **2**, 213-217.

Balazs, G.H. & Gilmartin, W.G. Unpublished data.

Berrill, J.J. (1950). *The Tuniccata*, The Royal Society: London.

Boden, B.P. & Kampa, E.M. (1964). Planktonic bioluminescence. *Oceanography and Marine Biology Annual Review*, **2**, 341-371.

Bleakney, J.S. (1965). Reports of marine turtles from New England and eastern Canada. *Canadian Field Naturalist*, **19**(2), 120-128.

Brongersma, L.D. (1969). Miscellaneous notes on turtles, IIB. *Proceedings of the Koninklijke Nederlanse Akademie Van Wetenschappen Series C*, **72**, 90-102.

Capra, F. (1949). La *Dermochelys coriacea* (L.) nel Golfo di Genovo e nel Mediterraneo (Testdu. Sphargidae). *Ann. Mus. Civ. Stor. Nat. Genovo*, **63,** 270-282.

Crisp, D.J. (1971). Energy flow measurements. In *IBP Handbook No. 16. Methods for the Study of Marine Benthos* (ed. N.A. Holme & A.D. McIntyre). Blackwell: Oxford.

Davenport, J. (1988). Do diving leatherbacks pursue glowing jelly? *British Herpetological Society Bulletin*, **24,** 20-21.

Den Hartog, J.C. & Van Nierop, M.M. (1984). A study on the gut contnets of six leathery turtles *Dermochelys coriacea* (Linnaeus) (Reptilia: Testudines: Dermochelyidae) from British waters and from the Netherlands. *Zoologische Verhanelingen Leiden*, **20,** 1-36.

Duron, M. (1978). Contribution à l'étude de la biologie de *Dermochelys coriacea* (Linné) dans les Pertuis Charentais. *Thèse Universite Bordeaux 3me cycle.* 1465.

Eckert, S.A., Nellis, D.W., Eckert, K.L. & Kooyman, G.L., 1986. Diving patterns of two leatherback sea turtles (*Dermochelys coriacea*) during interesting intervals at Sandy Point, St. Croix, U.S. Virgin Islands. *Herpetologica*, **42**(3), 381-388.

Holland, D.L., Davenport, J. & East, J. (1990). The fatty acid composition of the leatherback turtle *Dermochelys coriacea* and its jellyfish prey. *Journal of the Marine Biological Association of the United Kingdom*, **70,** 761-770.

Iverson, E.S. & Yoshida, H.O. (1956). Longline fishing for tuna in the Central Equatorial Pacific, 1954. *U.S. Fish and Wildlife Service, Special Scientific Report Fisheries No. 184* 33p.

Jones, E.C. & Shomura, R.S. (1070). Narrative report *Townsend Cromwell*, Cruise 44. *Bureau of Commercial Fisheries, Biological Laboratory, Honolulu.* Unpublished report, 1 pp.

Kashkina, A.A. (1986). Feeding on fishes of salps (Tunicata, Thalliacea). *Voprosy Ikhtiologii*, **3,** 440-447.

Marshall, N.B. (1979). *Developments in Deep Sea biology,* Blandford Press: Poole, Dorset, U.K.

Riley, G.A. & Gorgy, S. (1948). Quantitative studies of summer plankton populations of the Western North Atlantic. *Journal of Marine Research*, 7(2), 100-118.

Teissier, G. (1926). Sur la teneur en eau et en substances de *Chrysaora hyoscella* (L.) aux différents stades sont ontogénèse. *Bulletin Societe Zoologique Francais*, **51,** 266-273.

Annual Variations in Fecundity, Egg Size, and the Gonadal and Somatic Conditions of Queenfish *Seriphus politus* (Sciaenidae)

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Abstract. – Batch fecundity, weight-specific fecundity (number of eggs per gram somatic weight), size of ripe ovarian eggs, and the somatic and gonadal conditions of adult female queenfish *Seriphus politus* were estimated for five spawning seasons during an 8-year (1979–86) period. The effects of female somatic weight were evaluated in analyses of covariance comparing batch fecundity, egg size, and gonadal condition among years.

Batch fecundity was positively (and allometrically) related to female somatic weight. Fecundities were remarkably similar during four of the five years evaluated. After adjustment for annual differences in female size, fecundities were still significantly lower (by about one-fifth) during 1984, a major El Niño year, compared with the preceding (1979–80) or following (1985–86) pairs of years. Gonadal condition also was uniquely low in 1984. The 1984 declines in fecundity and gonadal condition co-occurred with low somatic condition during 1984, particularly for larger females. Mean size (diameter, dry weight) of eggs was indistinguishable among years. There was a positive relation between egg size and female body size, and a general decline in egg size as the spawning season advanced for females of all sizes.

Likely links between declines in fecundity, gonadal and somatic condition, and the crash in planktonic production during the 1982–84 El Niño are discussed.

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Few data exist on annual variations in reproductive traits (fecundity, egg size, gonadal allocation) of marine fishes. At a minimum, however, such data are necessary if fisheries ecologists are to begin to understand the many processes, including the vagaries of planktonic transport, that influence the large annual and longer-term temporal fluctuations in the recruitment and subsequent year-class abundance of marine fish stocks (Sinclair 1988, Bailey and Almatar 1989). The influences of egg size and quality on the early growth and survivorship of most species are poorly understood (Ware 1975).

The queenfish *Seriphus politus* is a small croaker abundant in the inner-shelf waters off southern California. It has planktonic egg and larval stages prior to the recruitment of juveniles to epibenthic habitat. Individual females are indeterminate serial spawners that produce as many as 20 batches of eggs during a protracted (6-month) spawning season (DeMartini and Fountain 1981). Juvenile and small adult, including male, queenfish feed on zooplankton (copepods and mysids), and large adults, females in particular, specialize on juveniles of the northern anchovy *Engraulis mordax* (DeMartini et al. 1985).

In this paper, I present data on batch and relative (weight-specific) fecundities, egg size, and the gonadal and somatic conditions of adult female queenfish collected during five spawning seasons spanning an 8-year period from 1979 to 1986. Fecundity, egg size, and condition indices are compared among years and related to concurrent variations in female body size. Because data are available prior to, during, and immediately following a major El Niño event, I interpret my observations in terms of known interannual variations in planktonic production and potential food limitation.

Methods

Sample collection

Queenfish were collected during the March–August reproductive seasons (DeMartini and Fountain 1981) of 1979, 1980, 1984, 1985, and 1986. Nighttime (2000–0200 hours), biweekly to fortnightly collections with a lampara seine, made at 5–16 m bottom depths at three longshore locations in San Onofre–Oceanside waters (DeMartini et al. 1985), were used to index the abundance and to describe the size (length, weight) composition of the nearshore queenfish stock. Sample fish for gonad analyses were provided by daytime lampara seining, otter trawling, and gillnetting at <16-m depths in the same area, and by screenwell samplings of the San Onofre Nuclear Generating Station, near San Clemente, California. Nighttime samples were used to characterize abundance and size composition, because net avoidance is less at night (Allen and DeMartini 1983). Fish analyzed for reproductive variables and condition were collected during daylight hours, because oocytes destined for imminent spawning are macroscopically recognizable within ovaries only as they hydrate during the half-day preceding dusk spawning (DeMartini and Fountain 1981).

Table 1

Size composition and catch-per-net-haul (CPUE) of adult female queenfish *Seriphus politus* collected during the March–August periods of 1979–86, off northern San Diego County, California. All fish were captured by lampara seines of consistent dimensions, mesh sizes, and method of deployment, during the night at 5–16 m bottom depths (DeMartini and Fountain 1981, DeMartini et al. 1985).

Year	SL (mm) $\bar{x}$	SL (mm) % >165 mm	Mean somatic wt (g)	Mean CPUE	Number Fish	Number Net hauls
1979	141	19	45	22	872	40
1980	134	16	40	22	995	45
1984	132	2	35	15	294	20
1985	134	6	38	20	624	32
1986	138	7	40	24	948	40

Processing of samples

Queenfish were refrigerated until processed within one day of collection. Sex and maturity were determined from macroscopic characteristics of gonads (DeMartini and Fountain 1981). Adult females were measured (standard length, SL, in mm), and their gonadectomized, wet body weights (as a proxy for somatic weight) were determined to 0.1 g.

Ovary and egg analyses

Both ovaries were removed (fresh) from adult females, weighed damp to 0.01 g, and, for fish in ripe(ning) condition, the presence of hydrated-state oocytes noted based on macroscopic criteria ("Stage 3" ovaries: DeMartini and Fountain 1981).

Hydrated-state ovaries were fixed and preserved in modified Gilson's Fluid (Bagenal and Braum 1971) for about three months, after which declines in oocyte diameters and dry weights should have stabilized (Witthames and Walker 1987). These specimens are hereafter referred to as "Gilson's-fixed." Batch fecundity was then determined for a maximum of 10 females per month and year of collection. Fecundity was estimated by gravimetric method (Bagenal and Braum 1971, DeMartini and Fountain 1981). Counts from each section were standardized to the total weight of both ovaries and then averaged (Hunter et al. 1985).

In a subsample of the Gilson's-fixed ovaries, I estimated the median diameter (random axis) of hydrated-state eggs: 10 randomly chosen oocytes per ovary pair were measured within ±25 μm (±1 "eyepiece unit" or "EU") using a compound microscope with ocular micrometer at 40× magnification. I examined a maximum of 10 females per month and year.

A linear dimension such as diameter might not accurately represent egg volume or mass because of variations in chemical composition or density (Blaxter and Hempel 1963). Therefore, I compared the diameter and dry weight of oocytes from Gilson's-fixed ovaries. For 46 females with hydrated-state ovaries present in March–August 1984 collections, I determined the mean dry weight of hydrated oocytes for one member of each ovary pair. I determined the mean diameter of hydrated oocytes for the other member of the ovary pair. Oocyte diameters were measured as described above. I determined mean oocyte dry weight by drying lots of 100 eggs to constant weight (1–2 days) in a vacuum jar over anhydrous calcium chloride. Eggs were dried at room temperature to avoid weight loss of volatiles (Hay 1984, Hislop and Bell 1987), and an aggregate weight determined to the nearest mg on an analytical balance.

Calculation of condition indices

The relative allocation of energy to gonadal tissue was indexed by the RGI of Erickson et al. (1985), as $\mathrm{RGI} = (G/W^b) \times 100$, where G = wet weight of ovaries in g, W = wet somatic weight in g, and b = the exponent of the power equation, $G = aW^b$. The relative gonadal index (RGI) is equivalent to $100 \times a$, where a is defined by the linearized (log-transformed) equation, $\ln G = \ln a + b \ln W$ (Erickson et al. 1985). It was necessary to adjust the gonadal index for somatic weight because the slope of the logarithmic gonad-to-somatic weight equation was significantly greater than one (i.e., the relation was allometric).

I first attempted to index somatic robustness as relative somatic condition, $K_n = CW/SL^b$ (Le Cren 1951), where W = wet somatic weight in g, SL = standard length in mm, C = a constant (10^5), and b = the exponent of the regression, $W = a\,SL^b$. However, the exponent, evaluated as the slope of the log-transformed weight-to-length equation $\ln W = \ln a + b \ln SL$, differed among years, thereby invalidating the use of such an index in analysis of covariance (Erickson et al. 1985, Cone 1989). I therefore limited my evaluation of robustness to comparisons of estimates of ordinary least-squares regression parameters (Cone 1989).

The relationship between wet and dry body weights might change throughout the spawning season (Love 1970). Therefore, I evaluated seasonal changes in dry somatic weight using 57 females collected at the start of (April–May, $n = 32$) and immediately following (August–September, $n = 25$) the 1985 spawning season. After ovarectomy, fish were frozen in air-tight "zip-lock" bags. Fish were then thawed, and each entire fish was macerated and individually oven-dried to a constant weight at 120°C for 24–32 hours.

Statistical analyses

I used nonparametric analysis of variance (Kruskal-Wallis One-way ANOVA) to compare the body lengths and somatic weights of females among years. Year was evaluated as a fixed-effect class variable, because I was interested in evaluating potential differences among a pre-established series of years. Analysis of covariance (ANCOVA) was used whenever possible to evaluate the effects of sampling year on batch fecundity, and on relative gonadal condition, after adjustment for year differences in somatic weight. A two-way Model I ANCOVA was used to evaluate subseasonal (approximately bimonthly) influences of egg diameter among years for females of differing body lengths. Dry egg weight was related to egg diameter by parametric regression. Dry somatic weight was regressed on wet weight for sample fish collected at the beginning and at the end of the 1985 spawning season; regressions were then compared using ANCOVA with body length as the covariate. Computations were made using the GLM, REGRESS and TTEST software procedures of the Professional Database Analysis System (PRODAS; Conceptual Software Inc. 1986).

Table 2

Summary statistics for adult female queenfish *Seriphus politus* used in analyses of reproductive variables and condition. Gonadal condition (RGI), batch fecundity, and egg diameter variables are least-square means (adjusted for annual differences in the body-size covariate). All variables, including fecundity, refer to sample females only. See Methods for explanations of the covariate used to adjust particular variables. One standard error is given in parentheses below each mean.

Year	*N*	SL (mm)	Somatic weight (W, g)	RGI[a]	Batch fecundity[b] (no. eggs)	Egg diameter[c] (EU)
1979	44	165	77	3.8	14,752	19.10
		(5)	(7)	(.2)	(1)	(.18)
1980	126	151	56	4.7	15,019	20.61
		(2)	(3)	(.1)	(1)	(.18)
1984	71	137	37	3.9	11,784	20.11
		(2)	(1)	(.2)	(1)	(.23)
1985	77	141	44	5.3	14,550	21.03
		(2)	(2)	(.2)	(1)	(.18)
1986	75	143	44	4.1	14,199	21.10
		(2)	(2)	(.2)	(1)	(.18)

[a] Estimates (± SE) of the exponent "b" in the power equation, gonad weight $(G) = aW^b$, were 1.185 ± 0.092 (in 1979), 1.162 ± 0.053 (1980), 1.232 ± 0.124 (1984), 1.280 ± 0.102 (1985), and 1.011 ± 0.102 (1986). Estimates did not differ among years, and were consistently greater than one (ANCOVA; ln somatic W × Yr interaction: $F_{4,383} = 0.87$, $P = 0.48$; pooled slope = 1.1810.

[b] Batch fecundity estimates were back-calculated from the means and SE's of ln-transformed data, multiplied by the correction factor of Sprugel (1983).

[c] Using the largest size-class of oocytes (ripe, hydrated-state) present in Gilson's-fixed ovaries (see Methods).

Results

Variations in female body size and CPUE

The size composition of the nearshore, adult female queenfish stock differed among years. Mean female length and weight were significantly lower in 1985 and especially 1984 (Kruskal-Wallis one-way ANOVA; both $P<0.001$). Large females (≥165 mm SL, chosen because they were relatively rare during 1984–86) in fact were nearly absent in 1984, when overall mean female abundance was at an estimated low (Table 1).

Females used in analyses of reproduction and condition also differed in mean body size (both somatic weight and length) among sample years (Kruskal-Wallis ANOVA, both $P<0.001$; Table 2).

Dry vs. wet somatic weight

The dry somatic weight of female queenfish averaged 24% of wet weight for fish collected at the beginning and at the end of the 1985 spawning season. Body length obviously influenced dry weight; subseason, however, had no significant effect on dry weight (ANCOVA of effects of body length and subseason on dry weight: length effect—$F_{1,54} = 346$, $P<0.0001$; subseason effect—$F_{1,54} = 0.42$, $P = 0.52$). Wet weight, therefore, could be used as an accurate proxy for dry weight throughout the queenfish spawning season, once adjusted for variations in female body size.

Batch fecundity

Batch fecundity in queenfish was positively related to female body size in each year (Table 3; Fig. 1). Fecundity was generally better related (based on higher R^2 values) to somatic weight than body length. Batch fecundity was disproportionately large in heavier females, as indicated by the value of the slope in the linear double-log plot (Fig. 1). Fecundity also differed among years, even after adjustment for annual differences in female size, with mean fecundity in 1984 significantly lower (by 20%) than mean fecundity in the other four years (Tables 2, 3, 5; Fig.1).

Table 3

Summary of ANCOVAs[a] testing the effects of female somatic weight and year on batch fecundity (F, no. eggs) and relative gonadal index (RGI). Both model R^2 are significant at $P<0.001$ (ln F, $R^2 = 0.694$; RGI, $R^2 = 0.114$).

Dependent variable	Source	df	*SS*	*MS*	*F*	*P*
ln F	ln W	1	118.1	118.1	693	<0.0001
	Yr	4	3.4	0.8	4.9	<0.0001
	Error	387	65.9	0.2		
RGI	ln W	1	0.06	0.06	0.03	0.87
	Yr	4	111	27.7	12.5	<0.0001
	Error	387	860	2.2		

[a] ln W × Yr interaction terms deleted for analysis of ln F ($P = 0.61$) and for analysis of the RGI ($P = 0.84$).

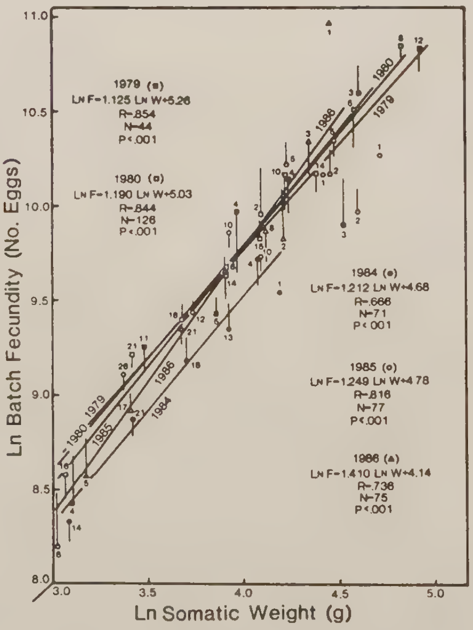

Figure 1

Relationship between the log of batch fecundity (ln F) and log female somatic weight (ln W) during each of the five study years. For illustration, mean fecundity data (+1 SE) are plotted for each 10-g weight class. The allometric equation, $F = aW^b$ (in log-linear form as $\ln F = \ln a + b \ln W$), and its summary statistics are provided for each fitted regression line.

Weight-specific fecundity

Patterns of weight-specific fecundity (WSF, no. eggs per g somatic weight) resembled those of batch fecundity. WSF appeared to increase with female body weight (ANCOVA of effects of somatic weight and year on WSF: weight effect—$F_{1,387} = 13.1$, $P<0.001$), and also seemed to vary among years ($F_{4,387} = 2.84$, $P = 0.025$). However, main effects were confounded by a weakly significant weight-by-year interaction ($F_{4,387} = 2.57$, $P = 0.038$). This heterogeneity of slopes prevented adjustments for annual variations in female weight and invalidated comparisons of intercepts among all five years. Although WSF generally increased with body weight, the disproportionate effect of larger females varied among years. Most notable was the particularly strong, positive influence of somatic weight on WSF in 1986. If the 1986 data are deleted and the ANCOVA analysis rerun, the slope heterogeneity disappears ($F_{3,310} = 0.82$, $P = 0.49$). When main effects are reanalyzed, a strong year effect ($F_{3,313} = 6.02$, $P<0.001$) becomes apparent, in addition to that of somatic weight. This year effect disappears ($F_{3,243} = 0.56$, $P = 0.57$) if the 1984 data are removed. Size-adjusted WSF in 1984 (mean ± SE = 264 ± 15 eggs per g) clearly was less than that in 1979, 1980, and 1985 (336 ± 8 eggs per g).

Diameter vs. dry weight of eggs

The median diameter of Gilson's-fixed, hydrated-state eggs was significantly related to the mean dry weight of these eggs (dry weight [in g, $\times 10^{-6}$] = 7.2 + 0.4931 egg diameter; $r = 0.47$, $n = 46$ females, $P = 0.001$). The mass of hydrated-state eggs therefore was approximately predicted ($R^2 = 0.22$) by egg diameter. While appropriate, I acknowledge that a more direct and accurate measurement of egg mass would have been preferable.

Egg size

Egg size varied with female body length and period within spawning season, with larger eggs produced by larger females, and all females producing larger eggs earlier in the season (Table 4; Fig. 2). The mean size of eggs did not vary among years, after adjustments for annual differences in female size and a significant period × year interaction (Tables 4,5). The latter interaction illustrates that the pattern of subseasonal decline in egg size varied among years (Fig. 2). Adjusted for female length, mean egg diameter appeared to vary 10% among years (Table 2). This difference in egg diameters, expressed in terms of volume (as $4/3\ \pi r^3$, the volume of a sphere), was 35% of the smaller value.

Table 4

Results of two-way ANCOVA testing the effects of female body length (SL, as covariate), study year (spawning season), and bimonthly period within the spawning season on size of ripe ovarian eggs. See Methods for explanation of egg size measurements. Model R^2 (0.510) significant at $P<0.001$.

Dependent variable	Source	df	*SS*	*MS*	*F*	*P*
Egg diameter	SL	1	57	57.0	22.5	<0.0001
	Period	2		{inestimable}		
	Yr	4		{inestimable}		
	Period × Yr	8	226	28.2	11.2	<0.0001
	Error	372	942	2.5		

Table 5

Summary of a posteriori Bonferroni *t*-tests for identity of year effects detected by ANCOVAs summarized in Tables 3 and 4. Means connected by underlines are not significantly different at $P = 0.05$. See Table 2 for values of adjusted means and SEs.

Variable	Year contrasts
ln F	1984 < 1985 = 1986 < 1980 < 1979
Egg diameter	1979 = 1984 = 1980 = 1985 = 1986
RGI	1979 = 1984 = 1986 < 1980 = 1985

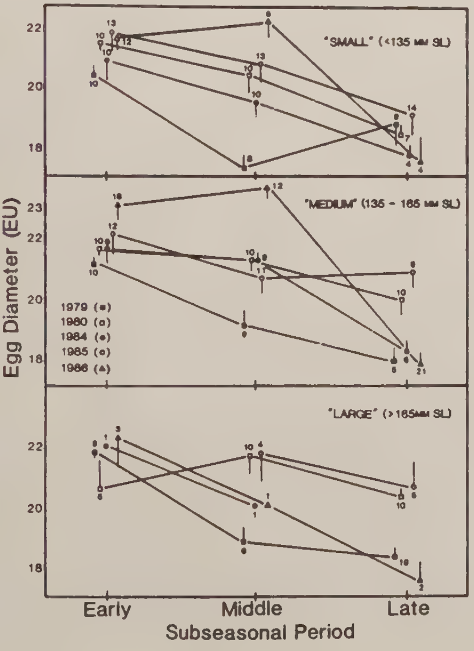

Figure 2

Relationship between mean (±1 SE) egg size (diameter of Gilson's-fixed, hydrated oocytes) and bimonthly period within spawning season for female queenfish of three arbitrary body sizes (small ≤13.5 cm, medium 13.6–16.5 cm, and large ≥16.5 cm SL), by sample year. See Tables 4 and 5 for results of ANCOVA testing the effects of subseasonal period (within year) on egg size, with female body lengths evaluated as a covariate. Data were pooled by bimonthly period to increase sample sizes.

Condition indices

Somatic condition varied with body size. Larger females usually were more robust (Table 6), but somatic condition also varied among years; the slopes and intercepts of length–weight relations were lower in 1984 and 1985 than in the other three years (Table 6). Larger females in particular were less robust in 1984 and 1985 (i.e., there was a highly significant ln SL × year interaction; Table 6), and this invalidated a straightforward interpretation of the effects of body size and year on a summary index of somatic condition.

As indicated by values consistently greater than one for the exponent "b" in the equation, $G = aW^b$, percentage gonad-to-somatic weight allocation increased for larger females (Table 2; Fig. 3). However, relative gonadal condition, as described by the RGI of Erickson et al. (1985) in which gonad weight has been standardized by female somatic weight, did not vary with female size (Table 3). The RGI did differ among years in concert with size-adjusted variations in fecundity; mean RGI in 1984 was about 14% lower than the RGI averaged over the other four years (Tables 2, 5). An identical pattern of annual variation in gonadal condition is observed if the classical gonadal index (GSI = [G/W] × 100) is used as the dependent variable in ANCOVA instead of the RGI.

Table 6

Least-squares regression parameters for length-weight relationships of adult female queenfish in each[a] of the study years. Ordinary least-squares regressions were calculated for the double-log transformed equation, $\ln W = \ln a + b \ln SL$, where $\ln a$ is the intercept and b is the slope.

	Intercept		Slope				
Year	Estimate	SE	Estimate	SE	R^2	N	P
1979	−11.864	0.246	3.151	0.048	0.990	44	<0.0001
1980	−11.660	0.178	3.106	0.036	0.984	126	<0.0001
1984	−10.450	0.378	2.853	0.077	0.952	71	<0.0001
1985	−10.433	0.206	2.862	0.042	0.984	77	<0.0001
1986	−11.888	0.616	3.152	0.124	0.898	75	<0.0001

[a] Estimated slopes of the $\ln W - \ln SL$ relations differed among years (ANCOVA; $\ln SL \times$ Yr interaction: $F_{4,393} = 6.10$, $P < 0.0001$).

Potential biases of condition indices

These differences in somatic and gonadal conditions were not the result of year variations in condition-selective collection methods. Lampara-seined fish comprised 84–100% of the specimens examined for condition in each year; among non-lampara fish, a maximum of 14% of the fish examined (in 1984) were collected by otter trawl. The somatic conditions ($K = 10^5 W/SL^3$; Le Cren 1951) of fish collected by lampara seine and otter trawl during April–June 1984, the only period when testable numbers of fish were collected using more than one method, were indistinguishable (seine: mean ± SE condition = 1.40 ± 0.016; trawl: mean ± SE = 1.39 ± 0.010; Student's $t = 0.28$, df = 151, $P = 0.78$).

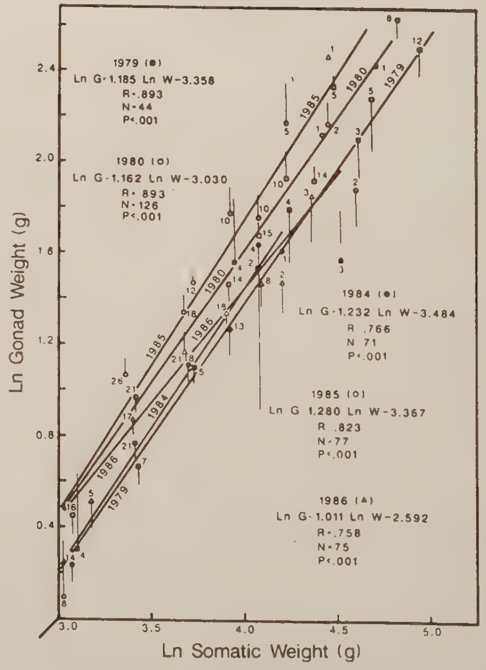

Figure 3

Relationship between the log of ovary weight (ln G) and log female somatic weight (ln W) during each of the five study years. For illustration, mean ovary weight data (+1 SE) are plotted for each 10-g weight class. The equation, $G = aW^b$ (in log-linear form as $\ln G = \ln a + b \ln W$), and its summary statistics are provided for each fitted regression line.

Discussion

Annual variations in body size

Interannual variations in the body size of adult female queenfish were marked, with the percentage contribution of large fish varying tenfold and mean somatic weights of the nearshore female stock varying by 25% over the study period. Clearly, potential year effects on fecundity and other size-sensitive variables are confounded with the effects of annual variations in body size, necessitating the use of size as a covariate in analyses.

Fecundity and female body size

During each of the queenfish spawning seasons monitored, batch fecundity was positively related to female body size, especially somatic weight. The overall mean value of b in the equation, $F = aW^b$ was 1.2087, which is significantly greater than unity.

In another detailed study, Parrish et al. (1986) detected allometric weight-specific fecundities in a size-(age-) structured stock of the northern anchovy. Empirical data for additional species of "weedy" (fast-growing, high-fecundity) fishes suggest that allometric fecundity-weight relations may be a general phenomenon (Blaxter and Hunter 1982, Clarke 1987). Reiss (1987), in a review and interpretation of relevant data, calculated that larger (older) fish in general have disproportionately large reproductive investments. Williams (1966), Wootton (1979), and Reiss (1987) have argued that disproportionate investments by older individuals should be adaptive for many iteroparous fishes with indeterminate growth. The queenfish data further suggest that allometry in gonadal allocation may be more common than is generally appreciated. Adjustments for allometry are required when calculating egg-based stock size estimates for species like queenfish and northern anchovy (Parrish et al. 1986).

Covariates of egg size

Egg size was positively related to queenfish body length, but declined for females of all sizes as water temperatures increased between the beginning (March–April) and end (July–August) of the spawning season. Egg size has been observed to increase with female body size, and decreases in egg size have been related to increases in water temperature during spring–summer production cycles, for diverse marine fishes (Williams 1967, Ware 1977, Blaxter and Hunter 1982 and references, Kashiwagi et al. 1985, Knutsen and Tilseth 1985, Daoulas and Economou 1986 and references, Imai and Tanaka 1987, Tanasichuk and Ware 1987). A positive female size–egg size relation and a seasonal decline in egg size with increasing water temperatures, the latter either ecophenotypic or genetic responses to the changing prey or predator (Clarke 1989) spectra confronting larvae, are now recognized as general phenomena in marine pelagic-spawners (Ware 1975; Markle and Frost 1985). It is obvious that estimates of mean egg size (and fecundity) must account for the effects of female body size and subseasonal variation.

Annual variations in fecundity and egg size

Batch fecundities of queenfish (adjusted for annual variations in female size) varied less than 6% during four out of the five years of this study. A marked change in batch fecundity, after adjustments for variations in female size, occurred only in 1984. Weight-specific fecundities paralleled batch fecundities.

Queenfish egg size varied little among the five years studied. Apparent egg volume averaged about 24% smaller in 1979 than during the other four years.

Few data exist on annual variations in the egg production of marine fishes (Bagenal 1957 and references, Antony Raja 1971, Pinhorn 1984, Hunter et al. 1985, Bailey and Almatar 1989). As one might expect, the size-specific fecundity of individuals varies among years, but sometimes fecundities are remarkably similar within a short series of years (Antony Raja 1971, Pinhorn 1984, Hunter et al. 1985). Observational and experimental studies (e.g., Tyler and Dunn 1976, Wootton 1979, Hunter and Leong 1981, Hay and Brett 1988) demonstrate that fluctuations in fecundity can and do result from naturally occurring food limitation. Food rations can also affect egg size (Hislop et al. 1978, Le Clus 1979). The trivial inference is that food can sometimes, although not invariably, limit egg production. Of greater interest is that, for queenfish, the maximum observed deviation from long-term average fecundity was only a 20% decline in a single year of unique oceanographic conditions, as described in the following section.

El Niño effects

The anomalously low fecundities and somatic condition of queenfish in 1984 occurred at a time when the 1982–84 El Niño was still evident in the Southern California Bight (McGowan 1985). During 1983–84, zooplankton production was at unusually low levels in inner-shelf waters (Petersen et al. 1986), mirroring the nadir in phyto- and zooplankton production in the California Current, farther offshore (McGowan 1985). This decline in planktonic production off southern California lagged the more extreme declines in production that resulted from the parent El Niño that occurred off the western coast of South America during 1982–83 (Barber et al. 1985).

During the 1982–84 California El Niño, tropical pelagic fishes migrated northward; many species became abundant off southern California, with some noted as far north as Washington–British Columbia (Smith 1985, Mysak 1986). El Niño effects on subtropical and cold-temperate fishes are poorly understood. Bailey and Incze (1985) and Mysak (1986) summarized the fragmentary data then available on distributional shifts and fluctuations in stock sizes of temperate fishes. Bailey and Incze (1985) speculated that El Niño effects on water temperature, nutrients, and planktonic production could effect egg and larval physiologies, disrupt the transport of early-life-history stages, and impact the somatic condition and egg production of adults. For vagile species, major impacts such as these should prompt movements to regions more favorable for growth and reproduction (Bailey and Incze 1985).

My data on interannual variations in body size composition suggest that large female queenfish (those individuals whose somatic condition and reproduction were particularly stressed by reductions in their anchovy prey) responded to El Niño conditions in part by emigrating out of the study area. The observed 1984 nadir in females >165 mm, followed by the return of fish of this size in 1985-86, demonstrates that emigration had to have occurred, because 165-mm long queenfish are more than 3 years-old (E. DeMartini, unpubl. data). Large fish might have emigrated to deeper depths, tracked colder water masses upcoast, or done both; unfortunately, lack of data prevent discrimination among these possibilities.

The only published evidence thus far for El Niño effects on adult fish condition and egg production off the west coast of North America are for the central stock of the northern anchovy (Fiedler et al. 1986), yellowtail rockfish *Sebastes flavidus* (Lenarz and Echeverria 1986), and for Pacific herring *Clupea harengus pallasi* (Tanasichuk and Ware 1987). In anchovy, individual egg production was lower in 1983-84 than in 1980-82 and 1985; this reflected lower spawning frequencies more than declines in batch fecundity (Fiedler et al. 1986). Specific fecundity (the daily production of eggs per unit biomass) of anchovy was low in 1983 (although high in 1984, the second El Niño year) compared with other years between 1980 and 1985. Growth rates of juvenile-adult anchovy were low in 1983-84 (Fiedler et al. 1986). For yellowtail rockfish off the central California coast, the visceral fat and gonad volumes of adults were lower in 1983 than in 1980 (Lenarz and Echeverria 1986). Off British Columbia, Pacific herring responded to the El Niño with increased batch fecundities coincident with reductions in mean egg size (Tanasichuk and Ware 1987). Adults of the anchovy and rockfish do not regularly occur in inner-shelf waters: most anchovy frequent the California Current, tens to several hundred kilometers offshore of central and southern California. Adult yellowtail rockfish are an epibenthic predator of continental borderlands offshore of the coasts of British Columbia-California.

It is tempting to speculate that the observed decrease in fecundity and somatic condition of queenfish during 1984 reflects lower production of the planktonic and anchovy prey of adults during a major El Niño year, compared with the 1979-80 and 1985-86 periods. If true, these data are among the first to show annual variations in egg production resulting from differences in size-specific batch fecundity, rather than changes in the duration of the spawning season or changes in the spawning frequency of females (Hunter et al. 1985). Interestingly, queenfish egg mass was not detectably lower in 1984, concurrent with the 20% decline in the number of eggs produced per batch, so the impact on egg production may have involved only the quantity, not the quality of eggs. Total number of spawnings per female season, whether due to changes in the duration of the spawning season or frequency of spawning by individual females, also might have varied for queenfish during 1979-86, but data are lacking. Length of spawning season and the interval between batches are unlikely to cancel out the batch fecundity pattern, though, since they might be expected to vary in concert with fecundity, if they covary at all (Hunter et al. 1985).

My observations also provide one of the first suggestions of food web impacts of the 1982-84 California El Niño on an inner-shelf fish species. Unfortunately, data on potential El Niño effects on the survivorship of early-life stages and year-class establishment are lacking for queenfish, as for offshore fishes. Future studies should concurrently measure survivorship and recruitment, together with population fecundity and egg production of the stock, in addition to individual fecundity and condition.

Acknowledgments

Many skilled technicians assisted in the collection of sample fish and in dissecting and processing ovaries. I especially thank S. Garner, K. George, G. Greenwald, and D. Opalenik. Special thanks go to R. Fountain, without whose diligent notekeeping this study would not have been possible. Also gratefully acknowledged are the constructive criticisms of T. Present and E. Schultz on drafts of the manuscript. Two anonymous reviewers contributed substantially to the improvements of draft manuscripts. This study was done in conjunction with complementary work funded by the Marine Review Committee, Inc., of the California Coastal Commission, and I thank the Committee for their support.

Citations

Allen, L.G., and E.E. DeMartini
1983 Temporal and spatial patterns of nearshore distribution and abundance of the pelagic fishes off San Onofre-Oceanside, California. Fish. Bull., U.S. 81:569-586.

Antony Raja, B.T.
1971 Fecundity fluctuations in the oil sardine *Sardinella longiceps* Val. Indian J. Sci. 18:84-98.

Bagenal, T.B.
1957 Annual variations in fish fecundity. J. Mar. Biol. Assoc. U.K. 36:377-382.

Bagenal, T.B., and E. Braum
1971 Eggs and early life history. *In* Ricker, W.E. (ed.), Methods for assessment of fish production in fresh waters, p. 166-198.

IBP (Int. Biol. Prog.) Handb. 3, Blackwell Sci. Publ., Oxford.

Bailey, K.M., and L.S. Incze
1985 El Niño and the early life history and recruitment of fishes in temperate marine waters. *In* Wooster, W.S., and D.L. Fluharty (eds.), El Niño North: Niño effects in the eastern subarctic Pacific Ocean, p. 143–165. Wash. Sea Grant Prog., Univ. Wash., Seattle.

Bailey, R.S., and S.M. Almatar
1989 Variation in the fecundity and egg weight of herring (*Clupea harengus* L.). Part II. Implications for hypotheses on the stability of marine fish populations. J. Cons. Cons. Int. Explor. Mer 45:125–130.

Barber, R.T., J.E. Kogelschatz, and F.P. Chavez
1985 Origin of productivity anomalies during the 1982–83 El Niño. Calif. Coop. Oceanic Fish. Invest. Rep. 26:65–71.

Blaxter, J.H.S., and G. Hempel
1963 The influence of egg size on herring larvae (*Clupea harengus* L.). J. Cons. Cons. Int. Explor. Mer 28:211–240.

Blaxter, J.H.S., and J.R. Hunter
1982 The biology of the clupeoid fishes. Adv. Mar. Biol. 20: 1–223.

Clarke, T.A.
1987 Fecundity and spawning frequency of the Hawaiian anchovy or nehu, *Encrasicholina purpurea*. Fish. Bull., U.S. 85:127–138.
1989 Seasonal differences in spawning, egg size, and early developmental time of the Hawaiian anchovy or nehu, *Encrasicholina purpurea*. Fish. Bull., U.S. 87:593–600.

Conceptual Software, Inc.
1986 PRODAS database, statistics, graphics: Manual and user's guide. Conceptual Software, Inc., Houston, Texas.

Cone, R.S.
1989 The need to reconsider the use of condition indices in fishery science. Trans. Am. Fish. Soc. 118:510–514.

Daoulas, C., and A.N. Economou
1986 Seasonal variation of egg size in the sardine, *Sardina pilchardus* Walb., of the Saronikos Gulf: Causes and probable explanation. J. Fish Biol. 28:449–457.

DeMartini, E.E., and R.K. Fountain
1981 Ovarian cycling frequency and batch fecundity in the queenfish, *Seriphus politus*: Attributes representative of serial spawning fishes. Fish. Bull., U.S. 79:547–560.

DeMartini, E.E., L.G. Allen, R.K. Fountain, and D. Roberts
1985 Diel and depth variations in the sex-specific abundance, size composition, and food habits of queenfish, *Seriphus politus* (Sciaenidae). Fish. Bull., U.S. 83:171–185.

Erickson, D.L., J.E. Hightower, and G.D. Grossman
1985 The relative gonadal index: An alternative index for quantification of reproductive condition. Comp. Biochem. Physiol. 81A:117–120.

Fiedler, P.C., R.D. Methot, and R.P. Hewitt
1986 Effects of the California El Niño 1982–1984 on the northern anchovy. J. Mar. Res. 44:317–338.

Hay, D.E.
1984 Weight loss and change of condition factor during fixation of Pacific herring, *Clupea harengus pallasi*, eggs and larvae. J. Fish Biol. 25:421–433.

Hay, D.E., and J.R. Brett
1988 Maturation and fecundity of Pacific herring (*Clupea harengus pallasi*): An experimental study with comparisons to natural populations. Can. J. Fish. Aquat. Sci. 5:399–406.

Hislop, J.R.G., and M.A. Bell
1987 Observations on the size, dry weight and energy content of the eggs of some demersal fish species from British marine waters. J. Fish Biol. 31:1–20.

Hislop, J.R.G., A.P. Robb, and J.A. Gauld
1978 Observations on effects of feeding level on growth and reproduction in haddock, *Melanogrammus aeglefinus* (L.) in captivity. J. Fish Biol. 13:85–98.

Hunter, J.R., and R. Leong
1981 The spawning energetics of female northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 79:215–230.

Hunter, J.R., N.C.H. Lo, and R.J.H. Leong
1985 Batch fecundity in multiple spawning fishes. *In* Lasker, R. (ed.), An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, *Engraulis mordax*, p. 67–77. NOAA Tech. Rep. NMFS 36.

Imai, C., and S. Tanaka
1987 Effect of sea water temperature on egg size of Japanese anchovy. Bull. Jpn. Soc. Sci. Fish. 53:2169–2178.

Kashiwagi, M., F. Nakamura, T. Okada, and N. Yamada
1985 A periodic variation of egg size of Japanese whiting *Sillago japonica* during the spawning season. Aquiculture 33:134–138.

Knutsen, G.M., and S. Tilseth
1985 Growth, development, and feeding success of Atlantic cod larvae *Gadus morhua* related to egg size. Trans. Am. Fish. Soc. 114:507–511.

Le Clus, F.
1979 Dry mass of yolked oocytes of the South West African pilchard *Sardinops ocellata* in relation to maturity stages and spawning cycles, 1972–1974. S. Afr. Sea Fish. Branch Invest. Rep. 119, 29 p.

Le Cren, E.D.
1951 The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). J. Anim. Ecol. 20:201–219.

Lenarz, W.H., and T.W. Echeverria
1986 Comparison of visceral fat and gonadal fat volumes of yellowtail rockfish, *Sebastes flavidus*, during a normal year and a year of El Niño conditions. Fish. Bull., U.S. 84:743–745.

Love, R.M.
1970 The chemical biology of fishes. Academic Press, London.

Markle, D.F., and L.-A. Frost
1985 Comparative morphology, seasonality, and a key to planktonic fish eggs from the Nova Scotian Shelf. Can. J. Zool. 63:246–257.

McGowan, J.A.
1985 El Niño 1983 in the Southern California Bight. *In* Wooster, W.S., and D.S. Fluharty (eds.), El Niño north: Niño effects in the eastern subarctic Pacific Ocean, p. 166–187. Wash. Sea Grant Prog., Univ. Wash., Seattle.

Mysak, L.A.
1986 El Niño, interannual variability and fisheries in the northeast Pacific Ocean. Can. J. Fish. Aquat. Sci. 43:464–497.

Parrish, R.H., D.L. Mallicoate, and R.A. Klingbeil
1986 Age dependent fecundity, number of spawnings per year, sex ratio, and maturation stages in northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 84:503–518.

Petersen, J.H., A.E. Jahn, R.J. Lavenberg, G.E. McGowen, and R.S. Grove
1986 Physical-chemical characteristics and zooplankton biomass of the continental shelf off southern California. Calif. Coop. Oceanic Fish. Invest. Rep. 27:36–52.

Pinhorn, A.T.
1984 Temporal and spatial variation in fecundity of Atlantic cod (*Gadus morhua*) in Newfoundland waters. J. Northwest Atl. Fish. Sci. 5:161–170.

Reiss, M.J.
1987 The intraspecific relationship of parental investment to female body weight. Functional Ecol. 1:105–107.

Sinclair, M.

1988 Marine populations: An essay on population regulation and speciation. Wash. Sea Grant Prog., Univ. Wash. Press, Seattle, 252 p.

Smith, P.E.

1985 A case history of an anti-El Niño to El Niño transition on plankton and nekton distribution and abundances. *In* Wooster, W.S., and D.L. Fluharty (eds.), El Niño North: Niño effects in the eastern subarctic Pacific Ocean, p. 121–142. Wash. Sea Grant Prog., Univ. Wash., Seattle.

Sprugel, D.G.

1983 Correction for bias in log-transformed allometric equations. Ecology 64:209–210.

Tanasichuk, R.W., and D.M. Ware

1987 Influence of interannual variations in winter sea temperature on fecundity and egg size in Pacific herring (*Clupea harengus pallasi*). Can. J. Fish. Aquat. Sci. 44:1485–1495.

Tyler, A.V., and R.S. Dunn

1976 Ration, growth, and measures of somatic and organ condition in relation to meal frequency in winter flounder, *Pseudopleuronectes americanus*, with hypotheses regarding homeostasis. J. Fish. Res. Board Can. 33:63–75.

Ware, D.M.

1975 Relation between egg size, growth, and natural mortality of larval fish. J. Fish. Res. Board Can. 32:2503–2512.

1977 Spawning time and egg size of Atlantic mackerel, *Scomber scombrus*, in relation to the plankton. J. Fish. Res. Board Can. 34:2308–2315.

Williams, G.C.

1966 Adaptation and natural selection. Princeton Univ. Press, Princeton, 307 p.

1967 Identification and seasonal size changes of eggs of the labrid fishes, *Tautogolabrus adspersus* and *Tautoga onitis* of Long Island Sound. Copeia 1967:452–453.

Witthames, P.R., and M.G. Walker

1987 An automated method for counting and sizing fish eggs. J. Fish Biol. 30:225–235.

Wootton, R.J.

1979 Energy costs of egg production and environmental determinants of fecundity in teleost fishes. Symp. Zool. Soc. Lond. 44:133–159.

SC/S89/Gen11

Molecular Analysis of mtDNA Types in Exploited Populations of Spinner Dolphins (*Stenella longirostris*)

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ABSTRACT

Stock structure of geographic forms of the spinner dolphin (*Stenella longirostris*) in the eastern tropical Pacific (ETP) is a conservation issue. These animals are incidentally killed during yellow fin tuna purse seining by US and international fleets, and mortality quotas apportioned by stock have been established by legislative act. Four management stocks of spinner dolphins in the ETP are currently defined on the basis of morphology and geographical distribution. However, recent work proposes that two of the stocks (the northern and southern 'whitebelly' spinners) comprise a broad zone of hybridisation or clinal integration between the neighbouring endemic 'eastern' spinner and the more typical spinners residing to the west and around the world in the tropics. If this hypothesis is true, evidence of current or recent gene flow between the neighbouring 'stocks' should be apparent. To investigate this, we conducted a molecular analysis of mitochondrial DNA (mtDNA) extracted from livers of 151 spinner dolphins from the ETP and 13 spinner dolphins from the Timor Sea. We also analysed mtDNA from 10 spotted dolphins from the ETP. Liver mtDNA from each animal was digested with six restriction enzymes to deduce the individual mtDNA haplotypes. Genetic distances were then inferred within the sample pool by comparison of the individual mtDNA haplotypes in a pair-wise fashion.

The results suggest the following three points: (1) The morphologically defined neighbouring eastern forms of ETP whitebelly spinners are not genetically distinct at the level of resolution of our analysis. We found no concordance of mtDNA haplotype with either the stock type of the school or individual morphology. The mean between-form distance was not significantly different from the two mean within-form distances. Thus, introgression is likely occurring (or has recently occurred) and significant genetic interchange can be inferred. (2) Mean within-school mtDNA diversity varied from school to school, and no clustering of certain haplotypes within specific schools was detected. (3) Timor Sea spinner and the spotted dolphins have unique mitochondrial genotypes likely characteristic of their geographic and genetic separation in the case of the spinner dolphins and their species-level separation in the case of the spotted dolphins. These findings reinforce the morphologically-based hypothesis of non-uniqueness of the whitebelly form and suggest that relatively more emphasis should be placed on conservation of the endemic and presumably locally adapted eastern form.

Keywords: spinner dolphin; spotted dolphin; eastern tropical Pacific; genetics; stock identity; morphology/anatomy; management; incidental capture.

INTRODUCTION

Common sense, as well as many national and international mandates, dictates that marine mammals be managed on the basis of population or breeding units. Good management demands knowledge of the genetic as well as the spatial and temporal aspects of intraspecific population structure. It also requires awareness of how exploitation may alter this structure (Larkin, 1981; Allendorf *et al.*, 1986). Intraspecific populations have been variously called geographic forms, stocks, races, etc. In many situations, the populations, isolated to some unknown degree, may harbor sufficient genetic uniqueness to provide adaptable advantages within their habitat and make them morphologically distinguishable, at least in the modal sense, from each other.

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Pelagic dolphins, primarily spotted dolphins (*Stenella attenuata*), spinner dolphins (*S. longirostris*), striped dolphins (*S. coeruleoalba*) and common dolphins (*Delphinus delphis*), are killed incidentally during fishing with purse seines for yellowfin tuna (*Thunnus albacares*) in the eastern tropical Pacific Ocean (ETP) (see Fig. 2). A total allowable annual kill of 20,500 animals is currently in force for the US purse-seine fleet (Marine Mammal Protection Act of 1972 [U.S.C. 1371 (a) (2)]). The total is apportioned to species and stocks[2]. The division of the stocks is based on morphology and to a lesser extent on distribution (Perrin *et al.*, 1985). In the case of the spinner dolphins, *S. longirostris*, four morphologic/geographic forms have been given stock status: Costa Rican, northern whitebelly, southern whitebelly and eastern (Perrin, 1975; Perrin *et al.*, 1985). These have formed the basis for management and assessment (Smith, 1983; Buckland and Anganuzzi, 1988). Neither tagging (Perrin *et al.*, 1979; Hedgepeth, 1985) nor genetic studies of allozymes (Sharp, 1981; Landino, 1987) have been successful in further clarifying the geographic boundaries for management purposes. Determination of exchange rates by tagging failed because of insufficient returns. Sharp's studies revealed too little electrophoretic variation to attempt a genetic definition of populations, whereas Landino's study revealed variation at seven loci but not significant departures from expected Hardy-Weinberg equilibrium values in populations subdivided by stock, possibly due to insufficient sample size. Consequently, the degree of genetic variation between the stocks and the isolation or interchange between them has been unknown for the spinner dolphins (and other dolphins) in the ETP.

In the most recent reviews of geographical variation in *Stenella* spp. in the eastern Pacific, Perrin *et al.* (1985) and Perrin (1990) hypothesised that the eastern form of *S. longirostris* constitutes a population adapted to local conditions and that the whitebelly spinner populations comprise a broad zone of hybridisation or clinal intergradation between the eastern form and the spinner dolphins of the Central and South Pacific. The latter closely resemble spinner dolphins in other tropical waters around the world (Fig. 1). They put forward two hypothetical models of evolution of the eastern form. The first model proposed differentiation in isolation during a Pleistocene cooling that may have established a trans-equatorial cool-water barrier isolating a part of the far eastern tropical Pacific. The other model suggested differentiation due to very strong selection in the oceanographically unique ETP (Au and Perryman, 1985). Characteristics of the eastern form that suggest it may comprise a locally-adapted population include pronounced morphological divergence from spinner dolphins in the rest of the world's oceans (small body and skull size, dark overall colouration obscuring the typical spinner colour pattern, and marked sexual dimorphism in shape of body and dorsal fin – Perrin, 1990) and differential life-history characteristics (breeding season – Barlow, 1984; ovulation rate, pregnancy rate, age at maturation and testis size – Perrin and Henderson, 1984). Ecological character displacement involving the spotted dolphin has been suggested as a possible mechanism for the differentiation (Perrin, 1984).

The first model proposes divergence in isolation. The whitebelly spinner forms might have arisen as a result of re-established contact and genetic interchange during the present interglacial period and thus would be a hybrid swarm. This model might involve a dynamic

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[2] In recent years, an additional 60,000 to 100,000 dolphins have been killed annually by purse seiners of other nations (e.g. Hall and Boyer, 1987).

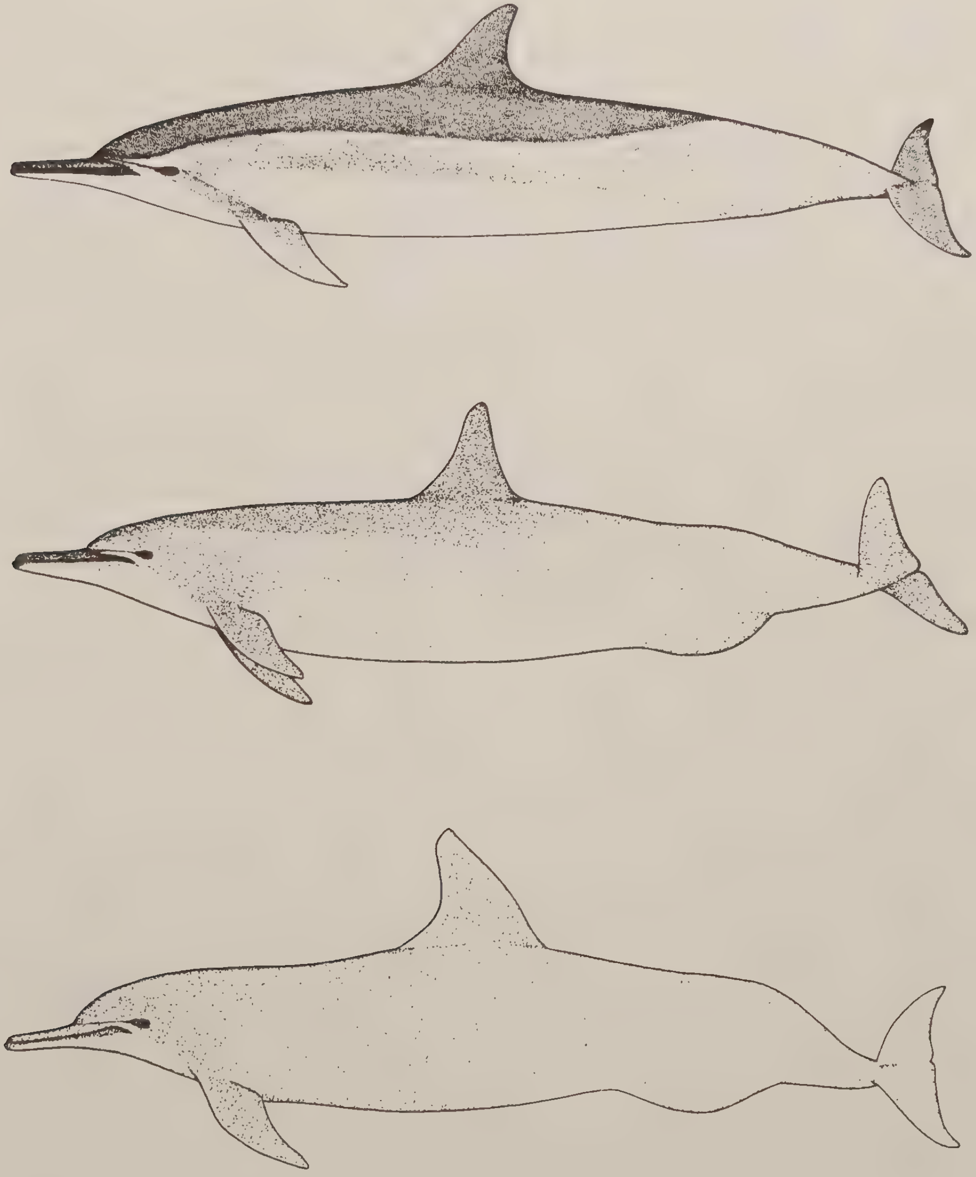

Fig. 1. Line drawing of modal appearances of the pantropical, whitebelly and eastern spinner dolphins (from Perrin, 1990).

situation, in which a much larger reservoir of 'ordinary' spinner dolphin genes located to the westward have been progressively replacing the relatively smaller eastern gene pool.

The second model proposes simple geographical differentiation without isolation. In this model, the whitebelly spinner populations might have evolved through clinal intergradation between the more primitive spinner dolphins of the Central and South

Pacific and the more specialised and derived eastern spinner dolphins. This presumably would be a relatively stationary situation in contrast to the first model. Both models propose that the whitebelly spinner form represents an intermediate form (either hybrid or intergrade) and predict substantial gene flow between the eastern and whitebelly spinner dolphin stocks.

The models proposing gene flow as an evolutionary force can be contrasted with an alternative and more conventional notion typically used in the management of marine species. This model would consider genetically isolated eastern and whitebelly stocks arising via: (1) isolation, the development of reproductive barriers, and, upon re-establishment of contact, no interchange; or (2) the slow accumulation of differences, establishing both morphological uniqueness and reproductive barriers (parapatric divergence). This hypothesis thus suggests that the whitebelly spinner form might be a relatively isolated population similar in that regard to the eastern form, rather than a hybrid form. This is the model closest to the actual current basis for management of the dolphins.

We chose to examine these alternative hypotheses of the origin of the eastern and whitebelly spinner forms (substantial gene flows vs. relative isolation) by means of mitochondrial DNA (mtDNA) analysis. The pattern of mtDNA diversity and concordance between the mtDNA genotype and the anatomic morphology, determined by the chromosomal DNA genotype, could be expected to differ between the two theoretical models. This assumption is based on observations that mtDNA can be exchanged between animal populations at a much higher rate than chromosomal DNA (Barton and Jones, 1983). Accordingly, little if any concordance between the distribution of mtDNA types and distribution of morphologic stocks might be expected in the first hypothesis postulating a substantial gene flow. In the second case, when DNA flow was halted due to reproductive isolation extending back to the Pleistocene or to parapatric divergence, some mtDNA clonal types should be unique to each population, at least those expected to have arisen since the isolation.

Quantitative genetic aspects of close taxonomic relationships can be studied through mtDNA sequence analysis. Nucleotide mutations occur about 10 times more frequently in mtDNA than in chromosomal DNA (Brown *et al.*, 1979; 1982), and therefore, analysis of mtDNA variability is more informative than the study of polymorphism in chromosomally encoded traits (Avise *et al.*, 1979b; for reviews, see Wilson *et al.*, 1985; Avise, 1986; Ferris and Berg, 1986; Avise *et al.*, 1987; Moritz *et al.*, 1987; Harrison, 1989). For the purpose of population analysis in mammals, mtDNA is assumed to be (i) inherited clonally from the female parent and (ii) identical in all somatic cells (homoplastic) (Avise *et al.*, 1987).

Our study deals with the distribution of mtDNA types among and between geographic forms and schools of the ETP spinner dolphins. We have evaluated whether these dolphins reproduce in isolation or exhibit indications of recent or ongoing reproductive interchange. For comparisons with the ETP spinner dolphins, we also obtained samples and measured mtDNA diversity of spinner dolphins from the Timor Sea off northern Australia and pantropical spotted dolphins from the ETP.

MATERIALS AND METHODS

Collection of samples

Samples for mtDNA analysis of spinner and spotted dolphins were collected by National Marine Fisheries Service and Inter-American Tuna Commission observers who regularly accompany US purse seiners fishing for yellowfin tuna and skipjack tuna (*Katsuwonus affinus*) in the ETP. In addition to their normal collection routine, observers were requested to collect and promptly freeze (-20°C) liver samples from dolphins that were accidentally suffocated in the nets during fishing operations. Samples were returned on dry ice from Panama, where the observers disembarked.

We accumulated a collection of tissue samples from 151 spinner dolphins and 10 spotted dolphins. Collection sites were distributed across the ETP, and the samples included both the eastern and whitebelly forms of the spinner dolphin. The sample sizes range from a single animal to twenty-one animals from the same school (Fig. 2). In addition, liver tissue from 13 spinner dolphins was obtained courtesy of the late Durant Hembree[3] from animals accidentally caught and suffocated in gillnets set for sharks in the Timor Sea (12°S, 127°E; Harwood and Hembree, 1987).

We assigned one of two stock types to each ETP spinner dolphin in the sample: eastern or whitebelly[4]. This school stock identification was based on the predominating appearance of the adult members of the school from which they were captured and is determined routinely by the biologists aboard the tuna seiners for the purpose of the mortality estimates. The eastern or whitebelly designation is sometimes difficult, because the areas of distribution of these two populations overlap and on rare occasions they are even captured in the same net-set. Even in areas where only so-called 'pure' schools are found, the individuals, especially in a whitebelly school, often demonstrate a wide range of

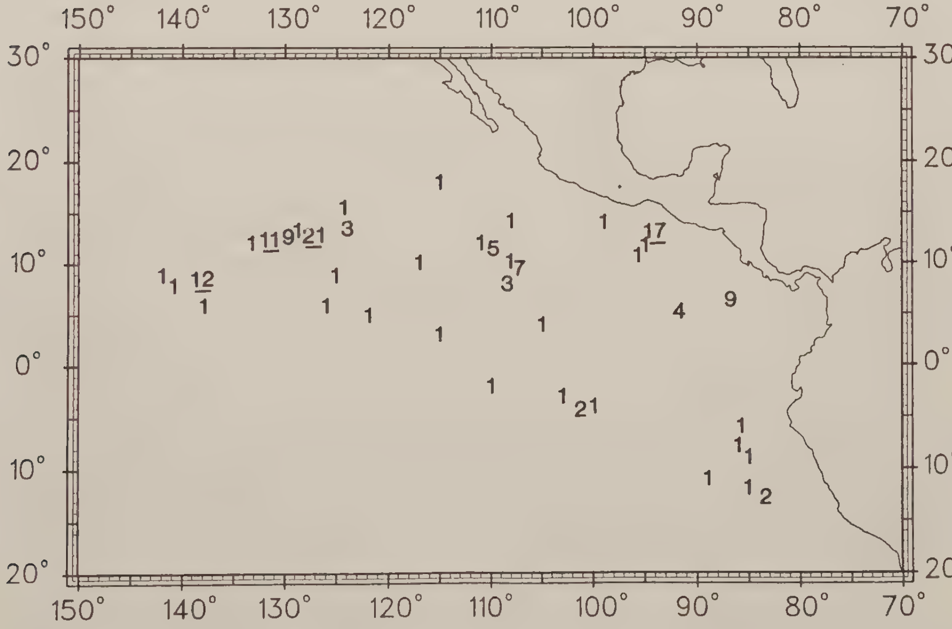

Fig. 2. Collection locations, including number captured from each school. These include eastern and whitebelly spinner dolphin as well as spotted dolphin samples (n=132). All two digit values are underlined.

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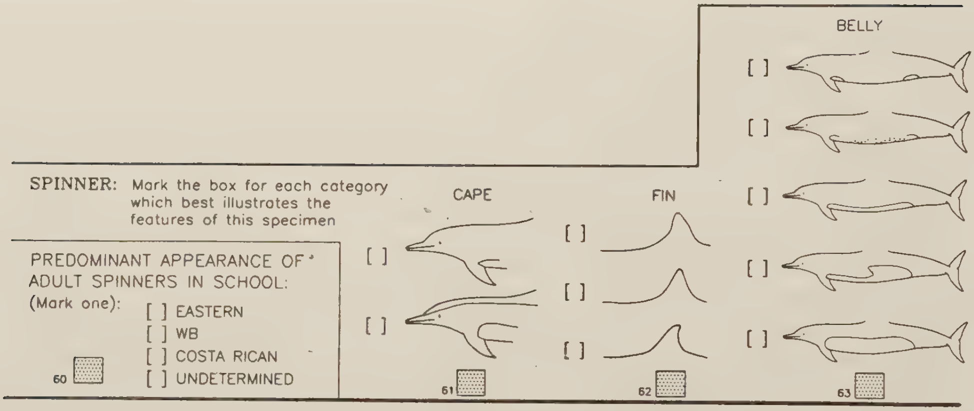
[3] Western Australian Museum, Perth, Western Australia, Australia 6000.

[4] The whitebelly spinner is further subdivided into northern and southern forms based on distribution, coloration and skull morphology (Perrin *et al.*, 1985). Our sample of 45 whitebelly spinners comprised 32 individuals captured from the northern area and 13 from the southern. For our analyses, we did not stratify below the whitebelly spinner level.



SPINNER: Mark the box for each category which best illustrates the features of this specimen

PREDOMINANT APPEARANCE OF ADULT SPINNERS IN SCHOOL:
(Mark one):
[ ] EASTERN
[ ] WB
[ ] COSTA RICAN
[ ] UNDETERMINED

Fig. 3. A reproduction of a portion of the form used by fishery observers on purse seines to record information about individual dolphins killed during the fishing operations. It illustrates the method used to assign a numerical score based on the physical characteristics of the individual animal. It is based on the ventro-lateral colour pattern (white in axilla and genital region = 1, to complete 'whitebelly' pattern = 5), fin shape (forward canted = 1, to falcate = 3) and the easily observable absence (=1) or presence (=2) of the cape. Animals scoring 10 are considered most 'whitebelly'-like. Animals scoring 3 are most 'eastern'-like. Note also that observers are asked to judge the predominant appearance of adult spinners in the school.

characteristics, and, as would be expected in sub-specific forms, sometimes a few individuals are observed that look much like those from the other population.

We felt it important to establish whether the mtDNA haplotype is related to the morphotype (individual physical appearance) or to the school designation. Therefore, we categorised our ETP spinner dolphin samples by assigning a numerical score based on a scale designed by one of us (WFP) using the physical characteristics of the individual (its morphotype) rather than the modal characteristics of its school (Fig. 3). This morphological score ranged from 3 (most 'eastern'-like) to 10 (most 'whitebelly'-like). Each specimen thus had two morphological designations, usually the same but sometimes different.

The Timor Sea dolphins resembled a typical pan-tropical spinner dolphin (Hawaiian spinner dolphin, cf. Perrin *et al.*, 1985). However, there is some evidence that these animals (as well as other China Sea, inshore spinner dolphins) may belong to a dwarf race, attaining sexual maturity at a much smaller size than do spinner dolphins in other regions (Perrin *et al.*, 1989). The spotted dolphins were all of the northern offshore type (Perrin *et al.*, 1985).

DNA isolation and restriction analysis

The quality of DNA samples from the specimens differed considerably, probably due to post mortem handling. The longer the interval between death and freezing of the tissue sample, the greater the amount of degradation of the DNA. We had no way of knowing how much time had elapsed between death in the net, retrieval of the corpse and extraction and freezing of the liver. Although we repeatedly attempted to purify mtDNA with density gradient ultracentrifugation, we never were successful in isolating pure mtDNA uncontaminated with chromosomal DNA. (Degradation of the mtDNA structure eliminates the buoyancy differences between the linear chromosomal DNA and the supercoiled mtDNA). Consequently, we resorted to isolation of total cell DNA, containing both the nuclear and mitochondrial. MtDNA, which comprises less than 0.1% of the total cell DNA, was then analysed by restriction mapping on Southern blots (Lansman *et al.*, 1981).

Total cell DNA was extracted using established protocols (Maniatis *et al.*, 1982), with some modification during the initial steps. Five grams of partially thawed liver tissue was minced with a razor blade and grated through taunt aluminium window screen directly into 20 to 30ml of iced 1X SSC. Cellular DNA was then prepared from SDS-solubilised cells by phenol/chloroform extraction and dialysis against a low salt buffer. The purified cellular DNA was diluted to a final concentration of 1mg/ml in a TE buffer (10mM Tris/HC1, 1mM EDTA, pH6.8) and stored at –70°C. Generally, 1 to 3mg of total cellular DNA were recovered from a 5g liver sample.

Two micrograms of the cellular DNA were used for each restriction enzyme digest. The digested DNA samples were resolved on horizontal 0.8% to 1.8% agarose gels. Two DNA fragment size standards (BRL 1kbp ladder and a recombinant mtDNA marker) were included in each gel with the dolphin DNA samples. The dolphin mtDNA fragments were visualised on Southern blots (S&S Nytron nylon membranes) using a mixture of cloned fragments of dolphin mtDNA collectively covering the entire mt genome (Southern *et al.*, 1988) as a probe. The recombinant mtDNA probe was labelled with ^{32}P by nick-translation to a specific activity of about 10^8cpm/μg. The blots were hybridised with the labelled probe ($2x10^6$cpm per blot) in the presence of 50% formamide, at 42°C, for 16 to 24hr. Stringently washed blots were then exposed to X-ray films with intensifying screens for 1 to 5 days.

Data analysis

The individual mtDNA sequence from each animal can be represented by a characteristic pattern comprised of restriction fragments generated by different enzymes. Animals showing identical composite fragment patterns are considered to belong to a single mtDNA lineage. Current models of mtDNA heredity in mammals assume that mtDNA lineage is matriarchal and clonal. The terms composite mtDNA genotype, lineage or haplotype are used here synonymously. Each different polymorphic pattern, produced by a given enzyme, was assigned an upper case letter. Considering all six enzymes, this permitted a six letter 'word' to represent each individual dolphin's composite mtDNA haplotype.

For population analysis, two approaches are generally used to analyse the relatedness of the haplotypes found within a sample: qualitative and quantitative (Avise *et al.*, 1979a,b; Lansman *et al.*, 1981; Johnson *et al.*, 1983). We employed the quantitative approach, where differences rather than similarities in the restriction patterns are compared. With this approach, mtDNA diversity is defined as sequence divergence between pairs of individuals expressed as base substitutions per nucleotide (p; Upholt, 1977). It is calculated from the proportion of the fragments shared (F) between individuals' multiband fragment patterns (Table 1). The value, F, is itself a measure of relative mtDNA difference between individuals (Avise *et al.*, 1979b; Lansman *et al.*, 1981),

$$F = (2N_{xy})/(N_x+N_y)$$

where N_x and N_y are the number of fragments in the digestion profiles of sample x and y, and N_{xy} is the number of fragments shared by the two organisms. The fewer fragments shared, the smaller the relatedness and the greater the sequence divergence,

$$p = 1 - \{[-F+(F^2+8F)^{\frac{1}{2}}]/2\}^{1/n}$$

Table 1

The letters designate each distinguishable restriction-fragment pattern produced by the given restriction endonuclease. The first five enzymes failed to show polymorphic patterns of restriction sites. The latter six did. Genome size did not in all cases add up to the approximately expected 16,300 value due to elimination of smaller than 700bp to 500bp fragments from the analysis; see text. Slight adjustments were made in the rounding of sizes to ensure that fragments that were not judged as having the same length did not have the same rounded value.

A specimen's 'haplotype' is assigned by combining the fragment pattern type of each enzyme into a six-letter composite word. For example, if a given specimen's DNA exhibited the *Bam*HI A pattern, the *Hpa*II A pattern, the *Hinc*II B pattern, the *Hinf*I A pattern, the *Ava*II A pattern and the *Hae*III A pattern, the haplotype word would be 'AABAAA'.

Enzyme	ID	Genome size	Fragment size
*Eco*RI	A	16.5	6.70,4.90,3.50,1.40
*SSt*I	A	16.5	5.80,3.40,2.60,2.50,2.20
*Bgl*II	A	15.7	6.00,3.70,3.50,1.30,1.20
*Ava*I	A	16.3	9.20,4.50,2.60
*Hind*III	A	16.6	5.70,2.80,2.60,2.00,1.80,1.70
*Bam*HI	A	16.1	9.50,5.60,1.00
	B	16.0	15.00,1.00
	C	16.1	9.50,4.15,1.40,1.00
	D	16.3	10.00,5.30,1.00
	E	16.2	5.60,5.50,4.10,1.00
	F	16.1	9.50,6.60
*Hpa*II	A	13.2	7.00,2.10,1.50,1.20,0.75,0.66
	B	13.2	6.90,2.10,1.50,1.30,0.75,0.66
	C	14.1	7.00,2.10,1.50,1.20,0.88,0.75,0.66
	D	12.5	7.00,2.10,1.50,1.20,0.66
	E	13.2	7.00,1.50,1.20,1.10,1.00,0.75,0.66
	F	13.9	7.00,2.10,1.50,1.40,1.20,0.66
	G	13.6	7.00,2.40,1.50,1.30,0.75,0.66
	H	14.4	6.90,2.30,1.50,2.30,0.75,0.66
*Hinc*II	A	16.4	6.20,4.00,3.50,0.92,0.88,0.58,0.35
	B	16.4	6.20,4.00,3.50,1.50,0.88,0.35
	C	16.2	10.00,3.50,1.50,0.88,0.35
	D	16.4	6.20,4.00,3.50,1.50,1.20
	E	16.8	4.20,4.00.3.50,2.40,0.92,0.88,0.58,0.35
	F	16.8	4.20,4.00,3.50,2.40,1.50,0.88,0.35
*Hinf*I	A	12.1	1.50,1.50,1.40,1.40,1.40,1.20,1.10,1.00,0.84,0.74
	B	12.4	1.50,1.50,1.50,1.40,1.40,1.40,1.10,1.00,0.84,0.74
	C	12.0	1.50,1.50,1.40,1.40,1.40,1.10,1.10,1.00,0.84,0.74
	D	13.1	2.40,1.80,1.70,1.50,1.50,1.40,1.20,0.84,0.74
	E	13.1	1.80,1.70,1.50,1.50,1.40,1.40,1.20,1.00,1.84,0.74
	F	12.5	1.80,1.50,1.50,1.40,1.40,1.20,1.10,1.00,0.84,0.74
	G	11.7	2.20,1.50,1.50,1.40,1.40,1.10,1.00,0.84,0.74
	H	11.0	1.50,1.50,1.40,1.40,1.40,1.20,1.00,0.84,0.74
	I	11.9	1.50,1.40,1.40,1.40,1.30,1.20,1.10,1.00,0.84,0.74
	J	12.1	2.60,1.60,1.50,1.50,1.30,1.10,0.92,0.84,0.74
	K	11.0	1.60,1.50,1.50,1.40,1.30,1.10,1.00,0.84,0.74
	L	11.9	2.40,1.60,1.50,1.50,1.30,1.10,0.92,0.84,0.74
	M	11.9	1.60,1.50,1.50,1.40,1.30,1.10,1.00,0.88,0.84,0.74
*Ava*II	A	15.8	9.00,3.50,2.80,0.54
	B	15.8	5.80,3.50,3.20,2.80,0.54
	C	16.0	4.20,3.50,3.20,2.80,1.80,0.54
	D	15.3	12.00,2.80,0.54
	E	16.0	6.70,4.20,2.80,1.80,0.54
	F	16.0	5.40,3.50,3.20,2.80,0.58,0.54
	G	16.0	4.40,4.20,2.80,2.30,1.80,0.54
	H	16.6	4.40,4.20,2.80,2.30,1.80,0.57,0.54

Table 1 continued.

Enzyme	ID	Genome size	Fragment size
*Hae*III	A	11.5	1.70,1.40,1.20,1.10,1.00,0.95,0.84,0.74,0.73
	B	10.9	1.70,1.40,1.20,1.10,1.00,0.95,0.84,0.74,0.73,0.63,0.59
	C	11.9	1.70,1.60,1.50,1.40,1.20,1.00,0.84,0.74,0.73,0.63,0.57
	D	11.5	1.70,1.40,1.20,1.10,1.00,0.95,0.84,0.74,0.73,0.69,0.59,0.57
	E	11.3	1.70,1.40,1.20,1.10,1.00,0.98,0.95,0.84,0.74,0.73,0.63
	F	10.8	1.70,1.40,1.20,1.10,1.00,0.95,0.84,0.74,0.73,0.59,0.57
	G	11.7	1.70,1.40,1.20,1.20,1.00,0.95,0.93,0.84,0.74,0.63,0.59,0.57
	H	10.6	1.70,1.40,1.20,1.10,1.00,0.95,0.74,0.73,0.63,0.59,0.57
	I	11.5	1.70,1.40,1.20,1.00,0.95,0.93,0.92,0.84,0.74,0.64,0.59,0.57
	J	11.9	1.70,1.50,1.40,1.20,1.00,0.95,0.84,0.74,0.73,0.63,0.59,0.57
	K	13.1	1.70,1.60,1.40,1.20,1.20,1.00,0.95,0.84,0.74,0.73,0.63,0.59,0.57
	L	11.2	1.70,1.40,1.20,1.00,0.95,0.84,0.80,0.74,0.73,0.63,0.59,0.57
	M	10.4	1.55,1.40,1.20,1.10,1.00,0.95,0.84,0.74,0.73,0.68,0.63,0.59,0.57
	N	9.6	2.00,1.90,1.70,1.40,1.20,1.10,1.00,0.99,0.86,0.74,0.63
	O	11.8	1.80,1.40,1.30,1.20,1.05,0.92,0.84,0.74,0.73,0.63,0.59,0.57
	P	11.3	1.80,1.50,1.30,1.20,1.05,0.92,0.84,0.74,0.73,0.63,0.59
	Q	12.8	1.80,1.40,1.30,1.20,1.05,0.96,0 92,0.84,0.74,0.73,0.66,0.63,0.57

The values of p must be calculated separately for each enzyme if length of the recognition sequence, n, varies (Lansman *et al.*, 1981). Values of n for the enzymes employed in this study are from Nei and Taijima, 1983. In our study, mean pair-wise values of p were collected and weighted by the total number of base pairs recognised by each type of enzyme (Ashley and Wills, 1987). We made estimates of sample variances of the mean pair-wise values of p by bootstrap methods, a nonparametric statistical procedure based on Monte Carlo sampling (see Appendix).

RESULTS

Restriction fragment polymorphism in mtDNA

Using an initial sample of 30 spinner dolphins, we found that 6 out of 13 tested restriction endonucleases were informative, revealing polymorphic fragment patterns consisting of 2 to 13 fragments (Table 1). Other tested enzymes either did not cut the mtDNA (*Kpn*I and *Xho*I) or failed to show polymorphic patterns of restriction sites (*Ava*I, *Bgl*II, *Eco*RI, *Hind*III, *Sst*I).

The informative six enzymes were used to digest DNA samples from 174 dolphins. Some restriction fragments, in particular those smaller than 500bp, were more difficult to visualise when yields of mtDNA were low (smaller fraction of mtDNA relative to chromosomal DNA) or background smearing was high due to the presence of degraded mtDNA. Therefore in the pattern analysis, fragments smaller than 700bp were not scored for *Hinf*I, 600bp for *Hpa*II, and 500bp for *Ava*II and *Hae*III. This was done to maximise the number of different samples analysed. In addition, individual samples were removed from the subsequent analysis if mtDNA bands in any of the six restriction digests were too faint or had too much background 'noise' to allow reasonably confident interpretation of the band pattern. After this adjustment, our reduced sample data base consisted of patterns of restriction fragments generated by the six enzymes, obtained from 143 of the animals.

Table 2

Number of individuals of all haplotypes listed for each stock sampled. The dashed lines connect stocks that share rare haplotypes (appearing only once in one of the populations). EE = eastern spinner dolphin stock designation; WB = whitebelly spinner dolphin stock designation; TIM = spinner dolphins from the Timor Sea; and SPOT = spotted dolphins.

	Stock	→	EE	WB	TIM	SPOT
	Sample size	→	79	45	11	8
1	AAAAAA		18	13		
2	AAAAAB		11	7		
3	AAAAAD		2			
4	AAAAAE		3			
5	AAAAAF		1			
6	AAAAAG		1	1		
7	AAAAAJ		2	1		
8	AAAAAK			1		
9	AAAAAN		1			
10	AAAADA		2			
11	AAABAA		6			
12	AAABAB		1			
13	AAACAA		1			
14	AAAFAA		1	1		
15	AAAFAB		3	1		
16	AAAGAA		1			
17	AAAHAE		1			
18	AAAIAA				2	
19	AABAAA				8	
20	AABAAB			1		
21	AACAAA			2		
22	ABAAAM		1			
23	ABABAD		1			
24	ABAKGO					1
25	ABAMGO					1
26	ACABAA			2		
27	ADABAA		1			
28	AEAAAA		1			
29	AGAAAL				1	
30	AHEJGO					2
31	AHEJGP					1
32	AHELGO					1
33	BAAAAD		1			
34	BAADBA			1		
35	BAAEBA			1		
36	BBADBA			1		
37	BBADBG		1	1		
38	BBBDBA		2			
39	BBBDBG		1			
40	BBBDBI		1			
41	BBBDFA			1		
42	BBBEBA			1		
43	BBBEBG		1	1		
44	BBBEBH			2		
45	BBBECA			1		
46	CAAAAB		3	1		
47	DBBEAA			1		
48	DBBECA		4			
49	DBBECG		4	1		
50	DBBEEG		1			
51	DBDECG		1			
52	DFABAC			1		
53	EAAAAB		1			
54	EHEJGQ					1
55	FHFJHO					1

In all, we observed 55 unique haplotypes in the reduced sample (Table 2). Frequencies of haplotypes by species and sample are given in Table 2. We found the haplotypes #24, #25, #30, #31, #32, #54 and #55 only in the spotted dolphin group, and #18, #19 and #29 only in the group of Timor Sea spinner dolphins. None of these haplotypes were found in the other 124 spinner dolphins from the ETP and none of the patterns found in them were found in the spotted or Timor Sea dolphin samples. Inspection of the haplotypes of the Timor Sea animals suggested that all of the individuals were closely related: 8 of the 11 animals had the haplotype #18; two, #19; and one, #29. A minimum of two point mutations, causing the gain/loss of two sites, inter-converts the haplotypes #18 and #19, and a minimum of four point mutations is required to inter-convert #18 and #29. The eight spotted dolphin samples showed much greater mtDNA diversity and none of the detected haplotypes predominated.

Correlations between mtDNA haplotypes and morphotypes

Within the ETP spinner samples, we found no correspondence between the mtDNA haplotype and either the school type or an individual's morphology. Intraspecific differences between spinner dolphin stocks (whitebelly or eastern) were not detected, whether stock identification was based on the individual morphotype or on the school stock. The most common haplotypes were #1 or #2. When stratified by stock (Table 2), 36% of the eastern sample vs. 45% of the whitebelly spinner sample exhibited the common haplotypes (#1 or #2) (n.s., chi$^{2}_{.05,1}$). When stratified by individual morphotype (Table 3), 35% of the animals with a morphotype index of 3 to 5 (very 'eastern'-like) exhibited the common haplotypes, 43% with an index of 6 to 8, and 39% with an index of 9 or 10 (very 'whitebelly'-like) exhibited the common haplotypes (n.s., chi$^{2}_{.05,2}$). Chi-square tests based on uncombined data either by the stock (2 x 55) or the morphotype (3 x 55), revealed no statistically significant heterogeneity. (See Roff and Bentzen, 1989, for chi-square analyses in situations where expected values within cells are very small).

Table 3

Number of individuals of all haplotypes listed for morphotype index. Totals do not add to 124, the number of ETP spinner dolphins, because some specimens did not have sufficient data to assign a morphotype score. A morphotype index of from 3 to 5 represents typical eastern spinner dolphin characteristics and from 9 to 10, typical whitebelly spinner dolphin characteristics. The dashed lines connect eastern and whitebelly morphotype groups that share rare haplotypes.

	Morphotype	→	3,4,5	6,7,8	9,10
	Sample size	→	49	21	36
1	AAAAAA		10	7	8
2	AAAAAB		7	2	6
3	AAAAAD				2
4	AAAAAE		2	1	
5	AAAAAF		1		
6	AAAAAG		1	1	
7	AAAAAJ		2		1
8	AAAAAK			1	
9	AAAAAN		1		
10	AAAADA		1	1	
11	AAABAA		4	1	
12	AAABAB		1		
13	AAACAA				1
14	AAAFAA		1	1	
15	AAAFAB			1	1

continued overleaf

Table 3 continued

	Morphotype → Sample size →	3,4,5 49	6,7,8 21	9,10 36
16	AAAGAA	1		
17	AAAHAE	1		
18	AAAIAA			
19	AABAAA			
20	AABAAB			1
21	AACAAA		1	1
22	ABAAAM			
23	ABABAD			
24	ABAKGO			
25	ABAMGO			
26	ACABAA			2
27	ADABAA		1	
28	AEAAAA	1		
29	AGAAAL			
30	AHEJGO			
31	AHEJGP			
32	AHELGO			
33	BAAAAD	1		
34	BAADBA			1
35	BAAEBA			1
36	BBADBA			1
37	BBADBG	1		1
38	BBBDBA	2		
39	BBBDBG	1		
40	BBBDBI		1	
41	BBBDFA			1
42	BBBEBA			1
43	BBBEBG	1		1
44	BBBEBH		1	1
45	BBBECA			1
46	CAAAAB	3		1
47	DBBEAA		1	
48	DBBECA	1		
49	DBBECG	3		1
50	DBBEEG			1
51	DBDECG	1		
52	DFABAC			1
53	EAAAAB	1		
54	EHEJGQ			
55	FHFJHO			

Application of a quantitative index of mtDNA diversity (p) emphasises what is apparent in the distribution of haplotypes (Table 4). The eight ETP spotted dolphins show obvious differences when compared to the ETP spinner dolphins. While the mean pair-wise mtDNA diversity within the group is similar to that of the eastern and whitebelly spinner dolphins (0.017, 0.012 and 0.015), the mean pair-wise mtDNA diversity between the spotted and the whitebelly spinner dolphins is 0.049, and between the spotted and the eastern spinner dolphins 0.044. The Timor Sea spinner dolphins when compared with the whitebelly and eastern spinner dolphins demonstrated much smaller between-group diversities, 0.011 and 0.009, respectively. The Timor Sea animals, as mentioned above, exhibit very little within-group mtDNA diversity (0.003).

The statistically inferred difference in mean pair-wise within-group mtDNA diversity of the two ETP spinner dolphin populations (0.012 vs. 0.015, Table 4), provides no extra information over that provided by a simple examination of the haplotype distribution. Insignificant mtDNA difference (0.014) is apparent between the samples stratified on school stock type. There is as much mtDNA diversity within the stocks as between them.

Table 4

MtDNA diversity among and within sample groups. Along the diagonal: within-stock sequence divergence (p, N, bootstrapped SD). Above diagonal: between sequence diversity (p, N, bootstrapped SD). EE = eastern spinner dolphin stock designation; WB = whitebelly spinner dolphin designation; TIM = spinner dolphins from the Timor Sea; and SPOT = spotted dolphins. One whitebelly animal was eliminated from the analysis due to uncertainty regarding shared bands (n=44).

	EE	WB	TIM	SPOT
EE	0.012 79 0.004	0.014 123 0.004	0.009 90 0.002	0.044 87 0.011
WB		0.015 44 0.005	0.011 55 0.003	0.049 52 0.016
TIM			0.003 11 0.002	0.038 19 0.008
SPOT				0.017 8 0.018

Diversity of mtDNA in schools

The mean within-school mtDNA diversity varied from school[5] to school. Measurements of the mean pair-wise mtDNA diversity for each school varied from zero to 0.023 (Table 5). Trends towards the clustering of certain haplotypes within specific schools were not detected (Table 6). The mtDNA diversity of each school sample was clearly independent of the size of the sample and the school size as estimated by the biologist on board the tuna vessel.

However, a weak tendency towards smaller diversities and smaller range of diversities was observed in the samples collected farthest offshore. Means of the average pair-wise mtDNA diversities from the offshore sets were 0.010 as compared to 0.015 for the inshore ones (Table 5). The range of the offshore sets was from 0.002 to 0.013, while that from the inshore sets was from 0.005 to 0.023. Some schools, like the Timor Sea sample, exhibited only a low level of mtDNA diversity and therefore appeared to have a highly specific 'tribal' character. In contrast, the character of other schools was less specific. The level of mtDNA diversity in such 'cosmopolitan' schools was equal to or greater than in the sample as a whole.

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[5] Tuna purse seiners generally set their nets on what are thought to be single schools. However, mixed schools of spinner and spotted dolphins are set on as well as occasionally mixed schools of eastern and whitebelly spinner dolphins. For simplicity, we are assuming that set is synonymous with school.

Table 5

Set (school) diversity showing stock identity of school, capture location, estimated school size and within-school sequence divergence (N, p, bootstrapped SD). Symbols after the p values indicate whether the mtDNA diversity of the school is greater than, less than, or equal to that of the stock sample as a whole (0.012 for the eastern spinner dolphin samples and 0.015 for the whitebelly). Schools 1-5 were captured in the outside region where the cumulative fishing pressure is half what it is in the inside region, where schools 6-11 were captured. EE = eastern spinner dolphin stock designation; WB = whitebelly spinner dolphin stock designation; and TIM = spinner dolphins from the Timor Sea.

Set	Stock	Position		School size	N	P	SD
a.	TIM	12°S	127°E	--	4	0.0	0.0
1.	WB	9°N	138°W	500	12	0.010<	0.066
2.	EE	12°N	130°W	400	11	0.012=	0.006
3.	EE	13°N	129°W	100	9	0.008<	0.005
4.	EE	13°N	128°W	900	21	0.013>	0.005
5.	EE	13°N	124°W	20	3	0.002<	0.001
Samples combined (schools 1 - 5)					56	0.010	0.003
6.	EE	11°N	110°W	200	5	0.007<	0.004
7.	WB	8°N	109°W	20	3	0.023>	0.010
8.	EE	10°N	108°W	150	7	0.022>	0.006
9.	EE	13°N	94°W	1900	16	0.009<	0.005
10.	WB	7°N	87°W	500	5	0.019>	0.007
11.	WB	6°N	87°W	750	4	0.005<	0.004
Samples combined (Schools 6 - 11)					40	0.015	0.005

DISCUSSION

The Timor Sea spinners and the spotted dolphins appear to have unique mitochondrial genotypes as suggested by the mtDNA haplotype analysis. Samples of these two dolphin groups, albeit small, contained haplotypes that were unique to group (Table 2).

Considering current theories of population genetics, it can be expected that differences between closely related but segregated populations would be manifested in the distribution of rare haplotypes that presumably arose uniquely in the dolphin groups. We detected eight cases of a rare mtDNA haplotype shared by the eastern and whitebelly spinner dolphin populations (Table 2). In five instances, the same rare mtDNA haplotype was found both in animals having the typical eastern morphotype and the whitebelly spinner morphotype (Table 3).

The detected evidence of mtDNA exchange between the forms is surprising considering the rather large differences in their morphology. However, it has been reported that in some cases mtDNA is transmitted across taxonomic barriers, particularly during breeding in zones of hybridisation between two species inhabiting overlapping geographical areas (Ferris *et al.*, 1983; Harrison *et al.*, 1987; Harrison, 1989; Wallis and Arntzen, 1989). The populations of spinner dolphins may display distinct morphological traits by virtue of differences in their chromosomal DNA types, which were not analysed in our study. Ferris *et al.* (1983) demonstrated that at the beginning of reproductive hybridisation between two species, the exchange of mtDNA types preceded the appearance of mixed chromosomal genotypes. It is therefore possible that the spinner dolphin populations have remained separated in their reproductive chromosomal genotypes and phenotypes, while their mtDNA types have become mixed due to recent mating between the groups. If such interbreeding indeed occurs, it can be expected that the resulting gene flow may evenually

Table 6

Number of individuals of all haplotypes listed for sets (schools) sampled; the stock designation of the school, the geographic position of capture and the sample size are also listed. EE = eastern spinner dolphin and WB = whitebelly spinner dolphin.

Set:	1	2	3	4	5	6	7	8	9	10	11
Stock:	WB	EE	EE	EE	EE	EE	WB	EE	EE	WB	WB
N:	12	11	9	21	3	5	3	7	16	5	4
1 AAAAAA	2	3	3	3			1	1	5	2	1
2 AAAAAB	4	3		2	1	1			4		
3 AAAAAD				2							
4 AAAAAE			1	1	1						
5 AAAAAF			1								
6 AAAAAG	1	1									
7 AAAAAJ			1	1						1	
8 AAAAAK											1
9 AAAAAN				1							
10 AAAADA				1		1					
11 AAABAA		1	1	1	1	1			1		
12 AAABAB						1					
13 AAACAA		1									
14 AAAFAA				1							1
15 AAAFAB	1		1						2		
16 AAAGAA				1							
17 AAAHAE								1			
18 AAAIAA											
19 AABAAA											
20 AABAAB	1										
21 AACAAA											1
22 ABAAAM									1		
23 ABABAD									1		
24 ABAKGO											
25 ABAMGO											
26 ACABAA											
27 ADABAA				1							
28 AEAAAA				1							
29 AGAAAL											
30 AHEJGO											
31 AHEJGP											
32 AHELGO											
33 BAAAAD								1			
34 BAADBA											
35 BAAEBA											
36 BBADBA	1									1	
37 BBADBG			1								
38 BBBDBA								2			
39 BBBDBG											
40 BBBDBI		1									
41 BBBDFA										1	
42 BBBEBA											
43 BBBEBG											
44 BBBEBH							1				
45 BBBECA											
46 CAAAAB	1			1		1					
47 DBBEAA							1				
48 DBBECA				1				1	2		
49 DBBECG		1		1							
50 DBBEEG								1			
51 DBDECG				1							
52 DFABAC	1										
53 EAAAAB				1							
54 EHEJGQ											
55 FHFJHO											

cause disappearance of the morphological differences between the two spinner groups, unless the morphological separation is maintained by strongly differential selection pressure. Such 'swamping out' of the eastern form, if it is occurring, may be facilitated by the relatively much greater depletion of the eastern population in the tuna fishery (Smith, 1983).

Although we feel that the evidence indicates the lack of complete isolation between the two forms, there does seem to be a weak indication of geographic partitioning of the haplotypes. As pointed out by S. Palumbi (pers. comm., University of Hawaii, December 1989), our approach is suitable for detecting strong patterns but leaves weak patterns undetected. To do so requires information about the relative relationship among the haplotypes. This is obtained by making gain/loss maps (Fig. 4). We only attempted this for the three enzymes producing the patterns with the fewest fragments: *Bam*HI, *Ava*II and *Hinc*II. Nevertheless, interesting patterns emerge.

If only the ETP samples are considered, it is clear from the gain/loss maps that individuals with patterns B & D for *Bam*HI; C & E for *Ava*II; or B, C & D for *Hinc*II form distinct clades. Then the 11 individuals with haplotype #48, #49, #50 and #51 would be remarkably divergent from one another. The eight eastern individuals having haplotype #48 and #49 seem to introduce a tremendous amount of 'noise' into the calculation of the pairwise genetic diversity. Removing those from the samples produces a distribution that is significantly different from random for both the *Bam*HI B & D clades and the *Hinc*II B, C & D clades (Table 7). Thus, setting aside the outlying rare haplotypes makes clear some concordance between differences in morphology and mtDNA.

In the analysis of mtDNA diversity in schools of spinner dolphins, we had expected to find that animals sampled from one school would be more related to each other than to members of other schools, and that the observed mtDNA diversity in samples pooled at the stock level would come from inter– rather than intra-school diversity. The variation in within-school diversity that we found, if not simply due to sampling error, may be related to fishing pressure. The offshore area (west of 115°W) has experienced about half the cumulative sets that the inshore area (east of 115°W) has since the beginning of purse-seine fishing in 1969 (Punsly, 1983). This may account for the greater within-school

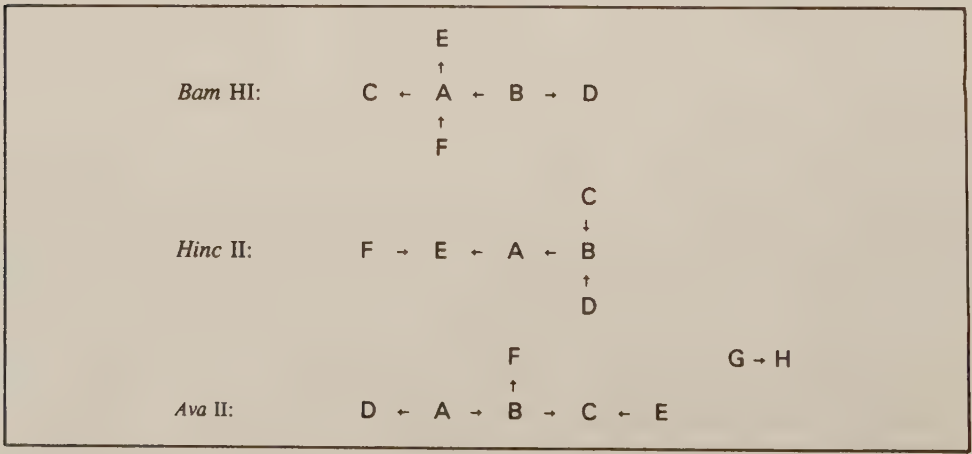

Fig. 4. Hypothesised restriction site gains and losses in *Bam*HI, *Ava*II and *Hinc*II. Patterns G and H in *Ava*II are found only in spotted dolphins in the sample and can not be related to the other patterns by the loss or gain of a single site.

Table 7

Results of goodness-of-fit tests for distribution of *Bam*HI clades B or D and *Hinc*II clades B, C or D with Haplotypes Nos 48 and 49 present and removed; see text. *Ava*II clades C or E were not present in sufficient numbers to test.

	Sample size		Frequency					
	EE	WB	Exp. EE	Exp. WB	Obs. EE	Obs. WB	Chi-sq.	Sig.
All samples								
*Bam*HI B or D	79	45	18.48	10.52	15	14	1.8018	n.s.
*Hinc*II B, C or D	79	45	15.29	8.71	13	11	0.9453	n.s.
Haplotypes Nos 48 & 49 removed from analysis								
*Bam*HI B or D	71	44	12.97	8.03	8	13	4.9698	<0.05
*Hinc*II B, C or D	71	44	10.50	6.50	6	11	5.0329	<0.05

diversity inshore. Purse-seine fishing requires herding of the dolphins with speed boats and most likely results in fragmenting of schools due to the chase or capture of partial schools.

We have suggested that Timor Sea spinner dolphins may comprise a unique group based on our measurement of their mtDNA diversity. Our sample size in this experiment was rather small, however, and may have introduced bias to interpretation of the results because, at most, only three different schools were represented (Table 6). The apparent uniqueness of the Timor Sea dolphins will therefore require further verification using a larger sample. However, it was suggested in other studies that local, isolated populations of spinner dolphins may exist in the far western Pacific Ocean. Perrin *et al.* (1989) reported a dwarf form of spinner dolphin in the Gulf of Thailand. These animals, likely mature, ranged in size from 120 to 137cm (n=10) compared with 157 to 235cm (n=2,309) in a sample of central and western Pacific Ocean spinner dolphins. The Timor Sea animals (of unknown maturity) from which our sample came ranged from 85 to 145cm (n=13).

Additional bias was introduced through selection of restriction enzymes for analysis of the mtDNA diversity. We supplemented our direct comparisons of the distributions of mtDNA haplotypes with the quantitative approach for measurement of sequence divergence (see Avise *et al.*, 1979b), but we used only those restriction enzymes which produced polymorphic patterns of restriction sites in the dolphin mtDNA. This biased enzyme selection was likely to result in overestimation of the level of mtDNA diversity within the spinner dolphin sample. Consequently, our measurements of mean pair-wise sequence divergence within the spinner dolphin sample cannot be directly compared to those from studies employing randomly selected enzymes with polymorphic as well as invariant restriction sites. However, our primary aim of detection of intraspecific differences in spinner dolphins was most effectively approached by the use of only such informative enzymes.

With the above *caveat*, our measurements of approximately 4% mtDNA divergence between the spinner and spotted dolphins is comparable to published data on mtDNA divergence at various taxonomic levels in other large or highly mobile animals. For example, six congeneric species of the horse family showed pair-wise values ranging from 3.3% to 7.8% (George and Ryder, 1986). In an extensive study of waterfowl species, the ranges of mtDNA diversity were 0.4% to 8.8% in nine *Anas* spp., 2.4% to 4.3% in four *Aythua* spp. and 10.9% between selected species belonging to different genera (Kessler and Avise, 1984). MtDNA diversity of 9.7% to 17.5% was measured between genera and subfamilies of galliform birds (Glaus *et al.*, 1980). Based on 19 genetic loci encoding liver and muscle enzymes, Shimura and Numachi (1987) showed that the degree of isozyme divergence at a given taxonomic level (local populations, species, genera and families) in toothed whales was low in comparison to small or non-mobile taxa but very similar to that in mobile avian ones.

We conclude that the study of mtDNA variability in spinner dolphins is consistent with the hypothesis that the eastern form represents a locally adapted gene pool and the whitebelly spinner forms a hybrid swarm. In a recently completed study of colour pattern and dorsal fin shape (Perrin *et al.*, in press) it has been found that samples from the whitebelly region exhibit greater variability (higher variance) in all characters than those from the core eastern region. This, and the intermediacy of the whitebelly form between the eastern and the pantropical form in other suites of morphological characters (Perrin, 1990), support the hybrid-swarm hypothesis. The hypothesis has significant implications for management. If the eastern spinner stock indeed represents a gene pool uniquely adapted to the ETP habitat, arguably it should receive more stringent protection than the hybrid whitebelly spinner dolphin stocks. This is especially true if the eastern spinner stock has been and currently is more heavily exploited than the whitebelly spinner stock, as indicated by past assessments (Smith, 1983; Buckland and Anganuzzi, 1988), because such skewed exploitation may amplify any trend towards the swamping of the unique eastern form by immigration from the west.

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REFERENCES

Allendorf, F., Ryman, N. and Utter, F. 1986. Genetics and fishery management: past, present and future. pp. 1–20. *In:* N. Ryman and F. Utter (eds.) *Population Genetics and Fishery Management*. University of Washington Press, Seattle and London. 420pp.

Ashley, M. and Wills, C. 1987. Analysis of mitochondrial DNA polymorphisms among channel island deer mice. *Evolution* 41:854–63.

Au, D.W.K. and Perryman, W.L. 1985. Dolphin habitats in the eastern tropical Pacific. *Fish. Bull., US* 83(4):623–43.

Avise, J.C. 1986. Mitochondrial DNA and the evolutionary genetics of higher animals. *Philos. Trans. R. Soc. Lond. (B Biol. Sci.)* 312:325–42.

Avise, J.C., Giblin-Davidson, C., Laerm, J., Patton, J.C. and Lansman, R.A. 1979a. Mitochondrial DNA clones and matriarchal phylogeny within and among geographic populations of the pocket gopher, *Geomys pinetis*. *Proc. NAS (U.S.)* 76:6694–8.

Avise, J.C., Lansman, R.A. and Shade, R.O. 1979b. The use of restriction endonucleases to measure mitochondrial DNA sequence relatedness in natural populations. I. Population structure and evolution in the genus *Peromyscus*. *Genetics* 92:279–95.

Avise, J.C., Arnold, J., Ball, R.M., Bermingham, E., Lamb, T., Neigel, J.E., Reeb, C.A. and Saunders, N.C. 1987. Intraspecific phylogeography: The mitochondrial DNA bridge between population genetics and systematics. *Annu. Rev. Ecol. Syst.* 18:489–522.

Barlow, J. 1984. Reproductive seasonality in pelagic dolphins (*Stenella* spp.): implications for measuring rates. *Rep. int. Whal. Commn* (special issue 6):191–8.

Barton, N. and Jones, J.S. 1983. Mitochondrial DNA: New clues about evolution. *Nature, Lond.* 306:317–8.

Brown, W.M., George, M. and Wilson, A.C. 1979. Rapid evolution of mitochondrial DNA. *Proc. NAS (U.S.)* 76:1,967–71.

Brown, W.M., Prager, E.M., Wang, A. and Wilson, A.C. 1982. Mitochondrial DNA sequences of primates: Tempo and mode of evolution. *J. Mol. Evol.* 18:225–39.

Buckland, S.T. and Anganuzzi, A.A. 1988. Estimated trends in abundance of dolphins associated with tuna in the eastern tropical Pacific. *Rep. int. Whal. Commn* 38:411–37.

Efron, B. and Tibshirani, R. 1986. Bootstrap methods for standard errors, confidence intervals and other measures of statistical accuracy. *Stat. Sci.* 1:54–77.

Ferris, S.D. and Berg, W.J. 1986. The utility of mitochondria DNA in fish genetics and fishery management. pp. 277–300. *In:* N. Ryman and F. Utter (eds.) *Population Genetics & Fishery Management*. University of Washington Press, Seattle and London. Washington Sea Grant Program. 420pp.

Ferris, S.D., Sage, R.D., Huang, C.M., Nielsen, J.T., Ritte, U. and Wilson, A.C. 1983. Flow of mitochondrial DNA across a species boundary. *Proc. NAS (U.S.)* 80:2290–4.

George, M. and Ryder, O.A. 1986. Mitochondrial DNA evolution in the genus *Equus*. *Mol. Biol. Evol.* 3:535–46.

Glaus, K.R., Zassenhaus, H.P., Fechheimer, H.S. and Perlman, P.S. 1980. Avian mtDNA: Structure, organisation and evolution. pp. 131–5. *In:* A.M. Kroon and C. Saccone (eds.) *The Organization and Expression of the Mitochondrial Genome*. North Holland Publishing, Amsterdam. 451pp.

Hall, M.A. and Boyer, S.D. 1987. Incidental mortality of dolphins in the eastern tropical Pacific tuna fishery in 1985. *Rep. int. Whal. Commn* 37:361–2.

Harrison, R.G. 1989. Animal mitochondrial DNA as a genetic marker in population and evolutionary biology. *Trends Ecol. Evol.* 4:6–11.

Harrison, R.G., Rand, D.M. and Wheeler, W.C. 1987. Mitochondrial DNA variation in field crickets across a narrow hybrid zone. *Mol. Biol. Evol.* 4:144–58.

Harwood, M.B. and Hembree, D. 1987. Incidental catch of small cetaceans in the offshore gillnet fishery in northern Australian waters: 1981–1985. *Rep. int. Whal. Commn* 37:363–7.

Hedgepeth, J.B. 1985. Database for dolphin tagging operations in the eastern tropical Pacific, 1969-1978, with discussion of 1978 tagging results. Southwest Fisheries Center Administrative Report No. LJ-85–03. Southwest Fisheries Center, La Jolla, California (unpublished). 40pp.

Johnson, M.J., Wallace, D.C., Ferris, S.D., Rattazzi, M.C. and Cavalli-Sforza, L.L. 1983. Radiation of human mitochondria DNA types analysed by restriction endonuclease cleavage patterns. *J. Mol. Evol.* 19:255–71.

Kessler, L.G. and Avise, J.C. 1984. Systematic relationships among waterfowl (Anatidae) inferred from restriction endonuclease analysis of mitochondrial DNA. *Syst. Zool.* 33:370–80.

Landino, S. 1987. Genetic variation of spinner and spotted dolphins (Genus *Stenella*) in the eastern tropical Pacific Ocean. Master's Thesis, University of Washington. 47pp.

Lansman, R.A., Shade, R.O., Shapira, J.F. and Avise, J.C. 1981. The use of restriction endonucleases to measure mitochondrial DNA sequence relatedness in natural populations. III. Techniques and potential applications. *J. Mol. Evol.* 17:214–26.

Larkin, P. 1981. A perspective on population genetics and salmon management. *Can. J. Fish. Aquat. Sci.* 38:1469–75.

Maniatis, T., Fritsch, E.F. and Sambrook, J. 1982. *Molecular Cloning (A Laboratory Manual)*. Cold Spring Harbor Laboratory, Cold Spring Harbor, New York. 545pp.

Moritz, C., Dowling, T.E. and Brown, W.M. 1987. Evolution of animal mitochondrial DNA: Relevance for population biology and systematics. *Annu. Rev. Ecol. Syst.* 18:269–92.

Nei, M. and Taijima, F. 1981. DNA polymorphism detectable by restriction endonucleases. *Genetics* 97:145–63.

Nei, M. and Taijima, F. 1983. Maximum likelihood estimation of the number of nucleotide substitutions from restriction sites data. *Genetics* 105:207–17.

Perrin, W.F. 1975. Distribution and differentiation of populations of dolphins of the genus *Stenella* in the eastern tropical Pacific. *J. Fish. Res. Board Can.* 32(7):1059–67.

Perrin, W.F. 1984. Patterns of geographical variation in small cetaceans. *Acta Zool. Fenn.* 172:137-40.

Perrin, W.F. 1990. Subspecies of *Stenella longirostris* (Mammalia: Cetacea, Delphinidae). *Proc. Biol. Soc. Wash.* 103(2):453–63.

Perrin, W.F. and Henderson, J.R. 1984. Growth and reproductive rates in two populations of spinner dolphins, *Stenella longirostris*, with different histories of exploitation. *Rep. int. Whal. Commn* (special issue 6):417–30.

Perrin, W.F., Evans, W.E. and Holts, D.B. 1979. Movements of pelagic dolphins (*Stenella* spp.) in the eastern tropical Pacific as indicated by results of tagging, with summary of tagging operations, 1969–76. NOAA Technical Report NMFS SSRF-737 (unpublished). 14pp.

Perrin, W.F., Scott, M.D., Walker, G.J. and Cass, V.L. 1985. Review of geographical stocks of tropical dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern Pacific. NOAA Technical Report NMFS 28 (unpublished). 28pp.

Perrin, W.F., Miyazaki, N. and Kasuya, T. 1989. A dwarf form of the spinner dolphin (*Stenella longirostris*) from Thailand. *Mar. Mammal Sci.* 5(3):213–27.

Perrin, W.F., Akin, P.A. and Kashiwada, J.V. In press. Geographic variation in color pattern and dorsal fin in the spinner dolphin, *Stenella longirostris*, in the eastern tropical Pacific.

Punsly, R.G. 1983. Estimation of the number of purse-seiner sets on tuna associated with dolphins in the eastern Pacific Ocean during 1959–1980. *Bull. IATTC* 18:229–99.

Roff, D.A. and Bentzen, P. 1989. The statistical analysis of mtDNA polymorphisms: chi-square and the problem of small samples. *Mol. Biol. Evol.* 6(5):539–45.

Sharp, G.D. 1981. Biochemical genetic studies, their value and limitations in stock identification and discrimination of pelagic mammal species. *FAO Fish. Ser. (5) [Mammals in the Seas]* 3:131–6.

Shimura, E. and Numachi, K.I. 1987. Genetic variability and differentiation in the toothed whales. *Sci. Rep. Whales Res. Inst., Tokyo* 38:141-63.

Smith, T.D. 1983. Changes in size of three dolphin (*Stenella* spp.) populations in the eastern tropical Pacific. *Fish. Bull., US* 81:1–14.

Southern, S.O., Southern, P.J. and Dizon, A.E. 1988. Molecular characterisation of a cloned dolphin mitochondrial genome. *J. Mol. Evol.* 28:32–42.

Upholt, W.B. 1977. Estimation of DNA sequence divergence from comparison of restriction endonuclease digests. 4(5):1257–65.

Wallis, G.P. and Arntzen, J.W. 1989. Mitochondrial-DNA variation in the crested newt superspecies: Limited cytoplasmic gene flow among species. *Evolution* 43:88–104.

Wilson, A.C., Cann, R.L., Carr, S.M., George, M., Gyllensten, U.B., Helm-Bychowski, K.M., Higuchi, R.G., Palumbi, S.R., Prager, E.M., Sage, R.D. and Stoneking, M. 1985. Mitochondrial DNA and two perspectives on evolutionary genetics. *Biol. J. Linn. Soc.* 26:375–400.

APPENDIX

Estimates of sample variances of the mean pair-wise values of p were made by bootstrap methods, a nonparametric statistical procedure based on Monte Carlo sampling (Efron and Tibshirani, 1986). In doing so, we attempted to deal with both error components of the mean pair-wise values: (1) the sampling variance associated with the selection of the sample from the population, and (2) the stochastic variance associated with the probabilistic methods for relating fragment information and nucleotide substitutions. Nei and Taijima, 1981 provide theoretical methods for calculating these variance components, however our data, derived from fragment rather than site information, does not meet the assumptions required by their methods. For the bootstrap methods we employed, the variance estimates must be viewed with caution for some of the small sample sizes.

The way we used the bootstrap concept to estimate variance was simple. The observed sample of (X_1, X_2,....X_N) allows (N/2)*(N-1) pair-wise comparisons of mtDNA diversity calculated from the patterns of restriction fragments generated by the six restriction enzymes. From these pair-wise comparisons, a mean can be calculated. For the bootstrapped estimate, an equal-sized sample is randomly drawn *with replacement* from the observed sample (X'_1, X'_2,...X'_N). And, a new six enzyme panel is randomly drawn, again with replacement, from the six enzymes, e.g. *Hpa*II, *Bam*HI, *Hin*fI, *Bam*HI, *Ava*II, *Hin*fI. Individual p values between individuals of the new bootstrapped sample are then recalculated using information from the fragment patterns generated by the six randomly chosen enzymes and from these, a mean pair-wise p value was determined. We repeated the process 1,000 times, and the distribution of resulting mean pair-wise p values was used to estimate the variance of the mtDNA diversities of original sample groups.

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Use of Corneal Cell Culture for R-Band Chromosome Studies on Stranded Cetaceans

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ABSTRACT

This paper presents a cell culture technique using corneas of postmortem animals and explores the application of fluorescent reverse banding (R-banding) chromosome analysis in stranded cetaceans. These techniques were used to look at heteromorphic (variable) regions in the karyotypes of five representative cetacean species which strand on U.S. coastlines: pygmy killer whale (*Feresa attenuata*); false killer whale (*Pseudorca crassidens*); short-finned pilot whale (*Globicephala macrorhynchus*); pygmy sperm whale (*Kogia breviceps*); and humpback whale (*Megaptera novaeangliae*). Numerous heteromorphic regions found in karyotypes of these species were compared with similar regions in karyotypes of bottlenose dolphins (*Tursiops truncatus*), a species for which extensive cytogenetic work has been done. An extra, unique chromosome was found in the karyotype of an individual *M. novaeangliae* which stranded in Hawaii. The results suggest that there are cytogenetic markers in these species that can be used, as they are in other cetaceans, to confirm relationships and examine regional population differences.

Introduction

Cytogenetic studies of stranded cetaceans have made an important contribution to the karyotypic data base for the Cetacea by providing an opportunity for chromosome analysis of species largely unavailable by other sampling methods (Arnason et al. 1977; Duffield 1977; Benirschke and Kumamoto 1978; Arnason 1980, 1981). To establish cell cultures for chromosome analysis, living tissue is essential. While sampling blood is a direct way of obtaining cells for standard leukocyte culture from live whales and dolphins (Duffield 1986; Duffield and Chamberlin-Lea 1990), obtaining viable, uncontaminated tissue samples from cetaceans dead for several days is a major problem. We have developed a technique for establishing cell cultures from the corneas of postmortem cetaceans. Corneal tissue has excellent regenerative properties associated with high mitotic indices (Van Horn et al. 1977; Leeson and Leeson 1981) and postmortem cornea can remain viable up to several weeks (Doughman et al. 1976).

Corneal cell cultures have been used for a variety of in vitro studies, including chromosome analysis (Conrad 1970; Dahl et al. 1974; Manski and Whiteside 1974; Pimenova and Simonenko 1974; Kenney et al. 1986). Cell cultures initiated from the corneas of postmortem cetaceans were used in this study to provide a supply of mitotic cells for chromosome preparations. These preparations were stained using a fluorescent reverse banding (R-banding) technique, which, in cetaceans, is particularly useful for chromosome studies because it bands euchromatic regions of the chromosomes for homologue identification and simultaneously visualizes highly variable heterochromatic regions (chromosome heteromorphisms) present in the chromosomes (Duffield 1986; Lambertsen and Duffield 1987; Duffield and Chamberlin-Lea 1990).

In this paper, we present R-band karyotypes derived from corneal cell cultures for five cetacean species which are periodically handled by stranding networks along the coast of the United States. The heteromorphic regions of the chromosomes from these species were compared with those of *Tursiops truncatus*.

Methods

Animals

The R-band karyotypes were prepared for four species that frequently strand on the east coast of Florida: pygmy killer whale ([*Feresa attenuata*], N = 1; field No. C-83-20, male, 215 cm, 10 July 1983); false killer whale ([*Pseudorca crassidens*], N = 2; field No. SWF-8631B, female, 259 cm, 5 June 1986; Id. No. SWC-PC- 8326, female, 312 cm, 25 February 1986); short-finned pilot whale ([*Globicephala macrorhynchus*], N = 2; field No. SWF-8651B, female, 356 cm, 24 July 1986; Id. No. SWC-GM-8003, female, 272 cm, 5 July 1983); and pygmy sperm whale ([*Kogia breviceps*], N = 1; field No. SWF-KB-8330-B, female, 272 cm, 18 September 1983). The R-band karyotypes were also prepared for a humpback whale ([*Megaptera novaengliae*], N = 1; male calf, SLP-Mn-81, 7 March 1981) stranded in Hawaii. Both blood and corneal cell cultures were available for one of the false killer whales and one of the pilot whales.

Collection of Corneal Samples

The eye was removed from the socket by severing the eye muscles, associated connective tissue, and the optic nerve, care being taken to ensure that the eye remained intact. Sterile precautions were not necessary during collection. The eye was stored and shipped dry in a plastic bag at 4°C until culturing; fluid in the bag encouraged tissue decomposition and increased the possibility of contamination. The inner corneal layers were kept moist by the aqueous humor, so desiccation of the cornea was not a problem.

Corneal Cell Culture

The eye was well rinsed in running tap water and placed cornea down in a 1:750 dilution of 17% aqueous Zephiran chloride (Winthrop Laboratories, New York, NY 10016) for 2 to 3 minutes. This procedure removed gross bacterial contamination from the corneal surface and did not appear to damage the inner cell layers. The cornea was carefully rinsed with distilled water to remove any traces of disinfectant.

A piece of cornea (ca. 3–4 mm diameter) was excised aseptically. To ensure maximum viability, two to three pieces were taken from different portions of the cornea. The inner portion of the cornea (including Descemet's membrane) and the associated endothelial cell layer occasionally separated from the stroma. This membrane and cell layer must be included for cell growth. The corneal sample was soaked for 1 hour in culture medium (Ham's F-10 with L-glutamine [Gibco, Grand Island, NY 14072] supplemented with 10–15% fetal calf serum; penicillin-streptomycin (Gibco), final concentration 100 units/mL; and Fungizone, amphotericin B (Gibco), final concentration 2.5 mcg/ml), which was further supplemented with 10 × concentrations of antibiotic and fungicide. The explants were minced, transferred to culture flasks, fed with culture medium and the cell cultures were placed in a 36°C, 5% CO_2-air incubator.

Cytogenetic Analysis

Metaphase cells were collected by the addition of colcemid (Gibco; final concentration 0.1 μg/mL) overnight. Cells were harvested by standard techniques (Hack and Lawce 1980) using a one part 0.075M KCl and one part 20% fetal calf serum hypotonic solution for 12 minutes at 37°C. Cells were fixed in three parts absolute ethanol and one part glacial acetic acid. Chromosomes were banded with a fluorescent R-banding technique using chromomycin A-3 and distamycin A (Sahar and Latt 1978; Schweizer 1980). Photographs, using Kodak Technical Pan 2415 film, were taken on a Zeiss microscope equipped with an ultraviolet light source and epifluorescence. Two to five karyotypes were prepared for each animal. In these karyotypes, the chromosome pairs were arranged into four groups (A–D) based on centromere position and numbered consecutively. The resultant karyotypes were examined for R-band heteromorphisms, discrete chromosomal regions which showed size and/or intensity differences between homologues. Chromosome composites were constructed based on the similarity in banding pattern of these species to *Tursiops truncatus*; the latter species was chosen as the stan-

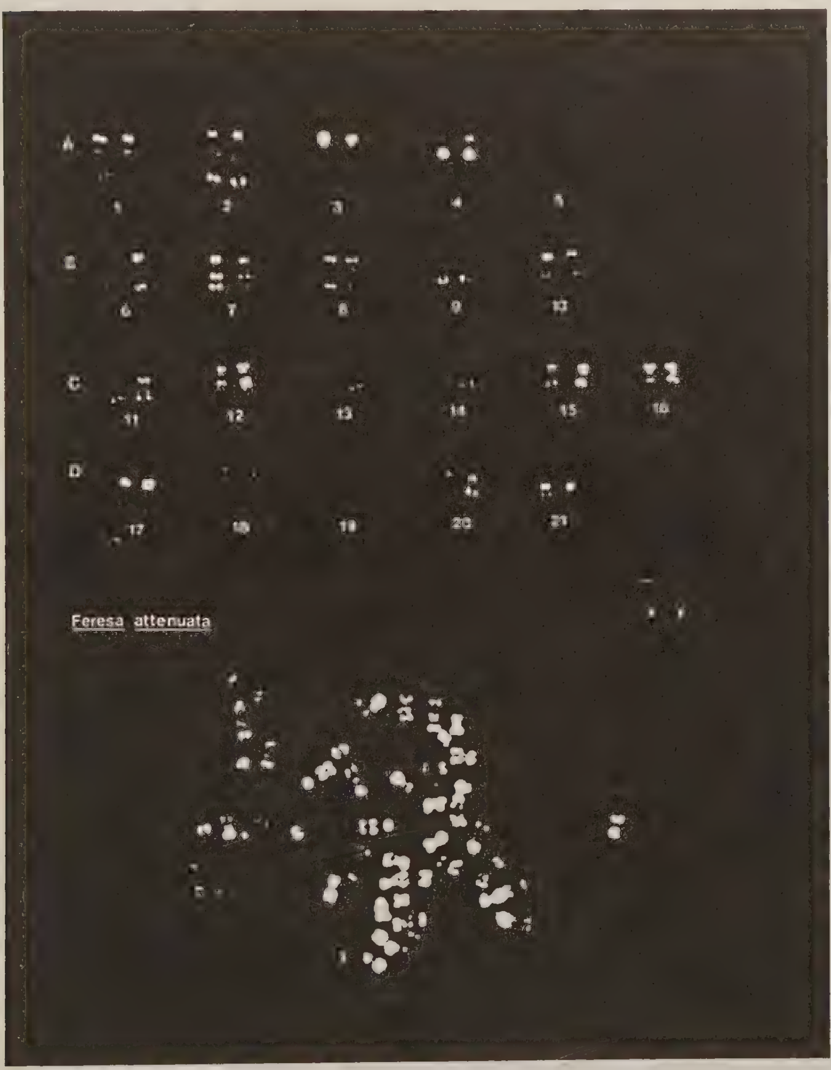

Figure 1
R-banded karyotype of a male *Feresa attenuata* (2N = 44).

dard because of its established R-band karyotype and range of heteromorphisms (Duffield and Chamberlin-Lea 1990). Differences among species in R-band heteromorphisms were noted.

Results

Cell cultures were established from eyes which varied in postmortem age from three days to two weeks. The corneal cells grew vigorously in culture. Outgrowth of cells from the original explant most commonly occurred within one day of the initiation of culture, no matter what the postmortem age of the eye. Significant amounts of cell migration from the explant were observed by the third or fourth days. For one eye, cell outgrowth was delayed for two or three weeks, but once established, this culture grew as well as those which had initially grown out more quickly.

The R-banded karyotypes of *F. attenuata*, *P. crassidens*, *G. macrorhynchus*, *K. breviceps*, and *M. novaeangliae* are shown in Figures 1–5. The *F. attenuata*, *P. crassidens*, and *G. macrorhynchus* karyotypes had a diploid chromosome number of 2N = 44. The *M. novaeangliae* calf had a 2N = 45 (+ mar), exhibiting an extra, small chromosome in its karyotype (Fig. 5). This chromosome stained faintly with R-banding and its origin was unknown, but it was consistently pres-

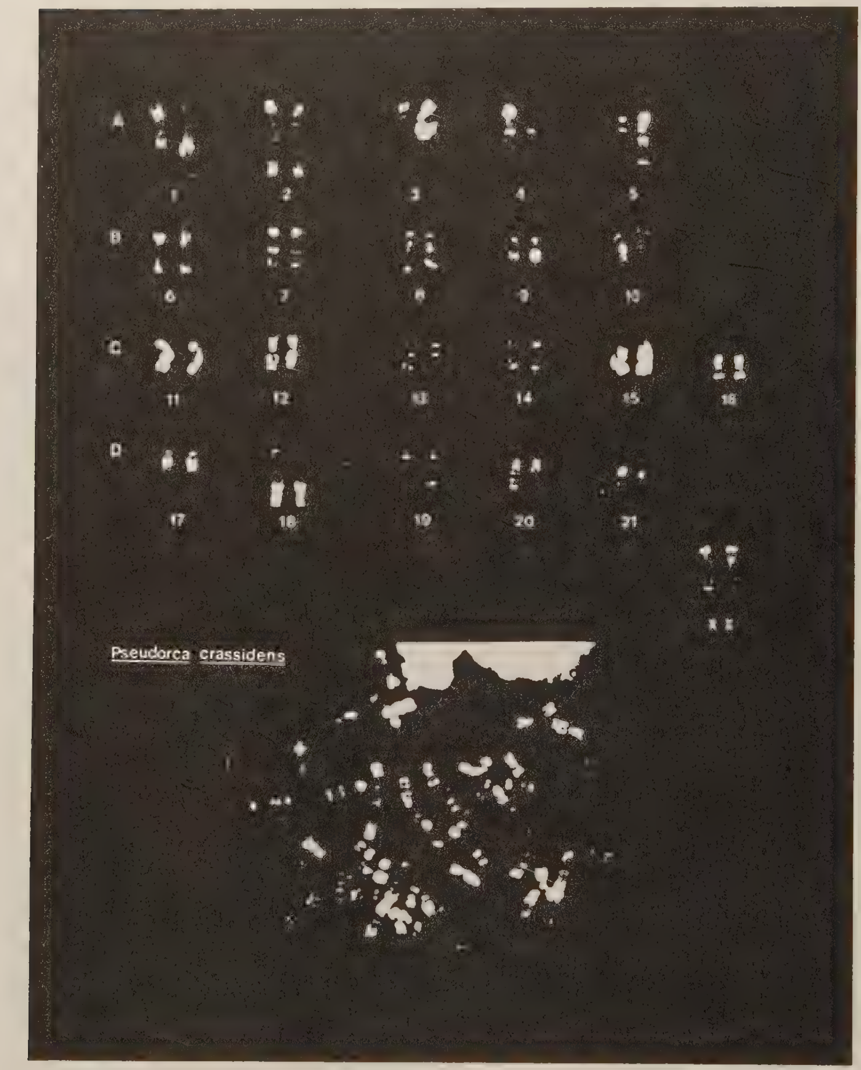

Figure 2
R-banded karyotype of a female *Pseudorca crassidens* (2N = 44).

ent in all cells examined. The karyotype of *Kogia breviceps* had a 2N = 42. For *P. crassidens* and *G. macrorhynchus*, the karyotypes obtained by corneal culture were consistent with those obtained from blood.

To compare the distribution of observed heteromorphic regions, a composite karyotypic comparison was constructed using one chromosome of each chromosome pair from the five species examined (Fig. 6). This composite included *Tursiops truncatus* as a standard because many individuals of this species have been examined by R-banding and both the distribution of heteromorphic regions and the type of variation found is well documented (Duffield and Chamberlin-Lea 1990).

Discussion

From the results reported here, as well as from several years of trials using corneal tissue to establish cell cultures for chromosome analysis in Duffield's laboratory, we have observed that prolonged postmortem viability, freedom from contamination and ease of handling make cornea an extremely useful tissue for establishing cell cultures from stranded cetaceans. We have found that the chances for viability are greatest when eyes are taken either from animals that washed ashore dead or from animals that were returned to the water prior to death. Animals dying out of the water more often exhibited decreased corneal cell

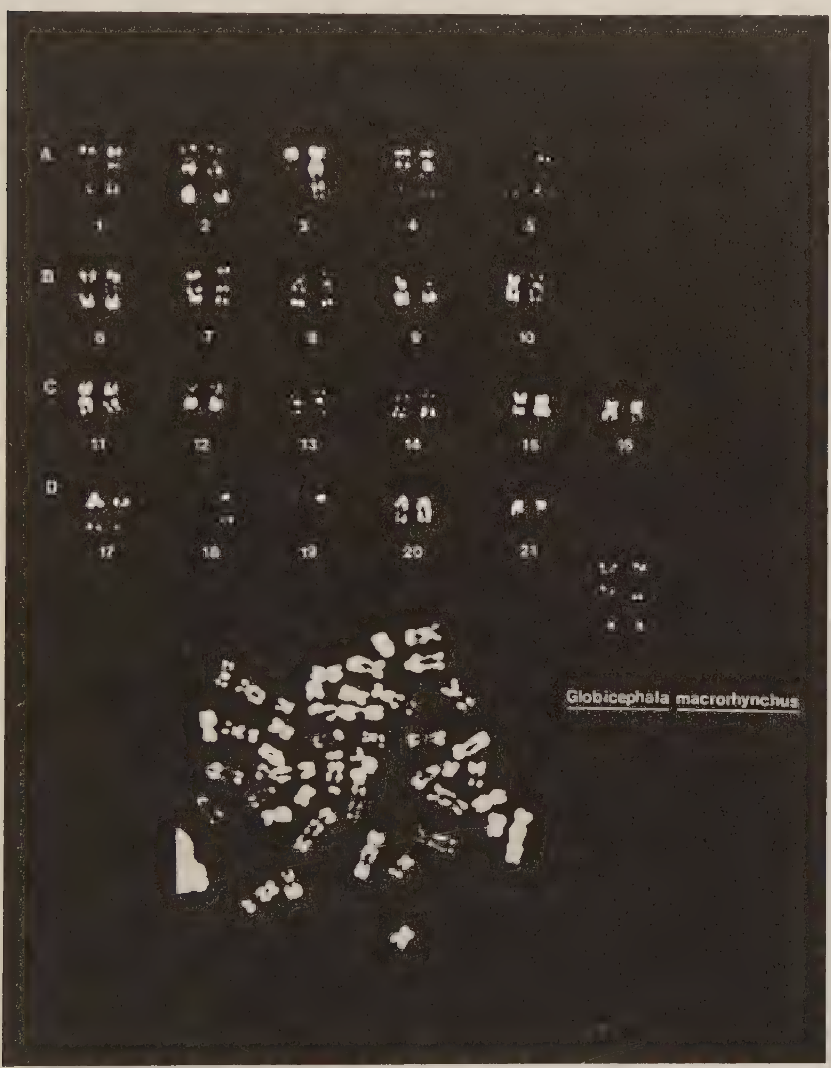

Figure 3
R-banded karyotype of a female *Globicephala macrorhynchus* (2N = 44).

viability, possible owing to extreme overheating (D. Duffield, pers. obs.). In contrast to other postmortem tissues, the inner cell layers of the cornea appear to remain uncontaminated until the eye has become severely decomposed. Because the eye can be removed intact from the animal and does not require sterile handling or preservation in culture media, samples are easy to obtain in the field.

Fluorescent R-band karyotypes have been previously reported for *M. novaeangliae* (Lambertsen and Duffield 1987; Lambertsen et al. 1988), but not for the other stranded species. The diploid number for *M. novaeangliae* is 2N = 44. The stranded calf examined here had a extra, small chromosome (2N = 45, + mar). The origin and significance of the extra chromosome seen in the karyotype of the stranded humpback whale calf is not clear, but a similar extra chromosome has been noted in a live Atlantic humpback whale that was sampled by skin biopsy (Lambertsen and Duffield 1987). An extra chromosome has also been reported for *T. truncatus* (Duffield et al. 1985; Duffield and Wells 1988). In this species, a small, unique marker chromosome was found in certain individuals belonging to a resident female bottlenose dolphin social unit in Sarasota Bay, FL. In contrast to the extra chromosome in the humpback whale, the extra chromosome in the bottlenose dolphin was brightly staining with satellites

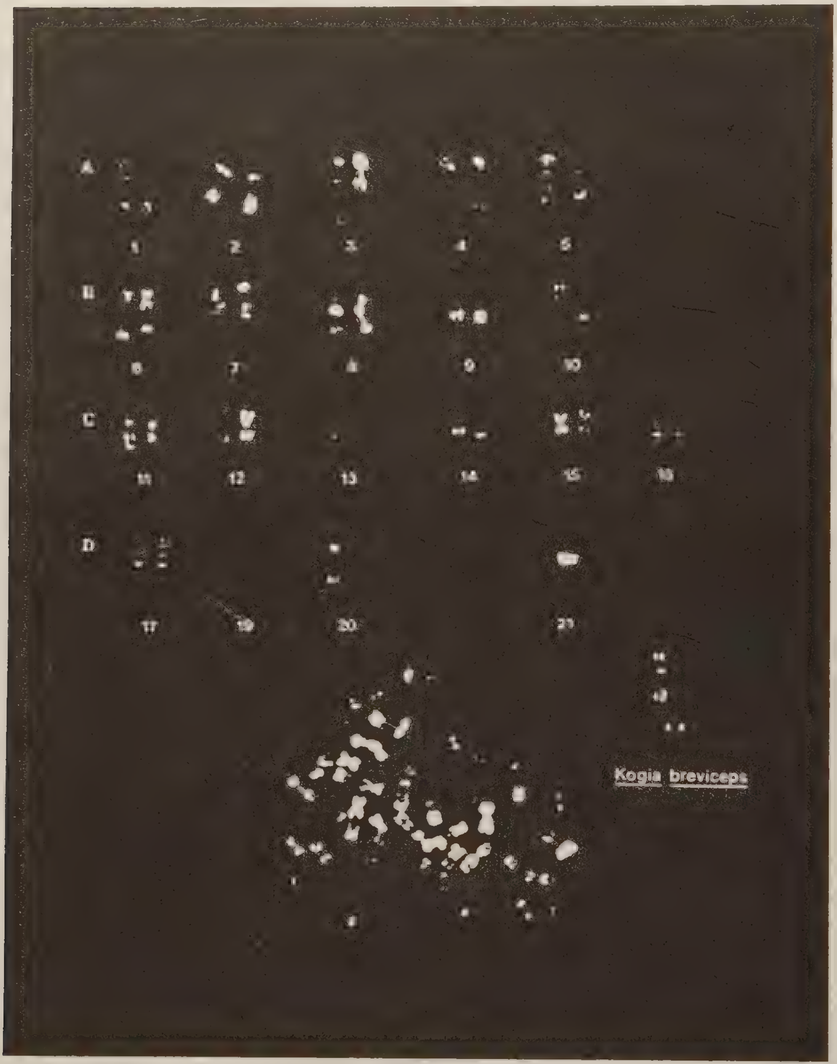

Figure 4
R-banded karyotype of a female *Kogia breviceps* (2N = 42).

and carried nucleolar organizer regions. This marker chromosome had been inherited for three generations and did not appear to have a phenotypic effect in any of the animals. The inheritance pattern of the marker confirmed long-term observational and behavioral data suggesting that resident female bands in the Sarasota study area were composed largely of related individuals (Wells et al. 1980; Irvine et al. 1981; Wells 1986). Because they are relatively rare and found in specific animals, these marker chromosomes are particularly useful for tracing the relationships and reproductive interactions of individuals and groups with neighboring or distant groups of the same species.

Although there were subtle differences in R-banding pattern among the five species examined here, their chromosomes were similar enough that the numbers on the chromosome pairs refer to the same homologous chromosome pair in each species. Pygmy sperm whales, as well as sperm and beaked whales, have a chromosome number of 2N = 42 (Arnason and Benirschke 1973; Arnason et al. 1977; Duffield 1977). A fusion between two of the acrocentric chromosome pairs may account for the 2N = 42 karyotype of *K. breviceps* (observation from the visual comparison of the R-band karyotypes, Fig. 6). However, detailed banding analyses have not been completed to determine the extent of similarities and differences in R-banding

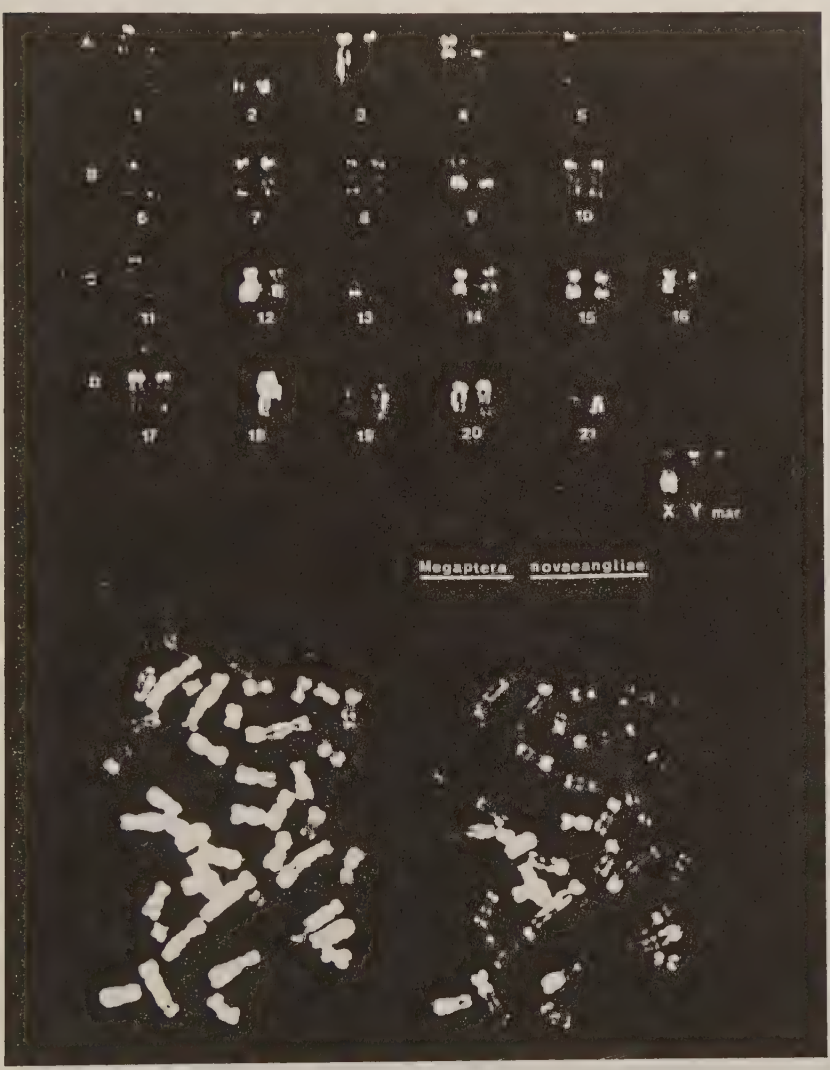

Figure 5
R-banded karyotypes of a male *Megaptera novaeangliae* (2N = 45, + mar). Two intensities of the metaphase spread for *M. novaeangliae* are included to show the faint staining extra chromosome. The presence of this extra chromosome was confirmed with standard Giemsa staining (not shown).

patterns and the basis for the change in number in *K. breviceps*. Instead, this paper concentrates on the presence in these species' karyotypes of chromosomal heteromorphisms which are visualized by R-banding.

Chromosome heteromorphisms have been noted in cetacean karyotypes both by C-banding (Arnason 1974, 1980; Arnason et al. 1977, 1980, 1985; Duffield 1977; Stock 1981; Worthen 1981) and fluorescent R-banding (Duffield 1982, 1986; Lambertsen and Duffield 1987; Duffield and Chamberlin-Lea 1990). C-banding is a chromosome banding technique that leaves tightly coiled C-band positive areas of the chromosome darkly stained (Bradbury et al. 1981) but denatures euchromatic regions. It, therefore, requires the sequential application of an additional banding technique (such as G-banding or R-banding) to identify homologous chromosome pairs. Fluorescent R-banding, in contrast, uses a staining agent which binds to guanine-cytosine (GC) rich DNA areas of the chromosomes. It bands euchromatin areas for homologue identification, while simultaneously binding strongly to GC-rich heteromorphic (variable) regions (Schweizer 1980). A significant number of GC-rich heteromorphic regions have been reported in the chromosomes of cetacean species (Duffield 1986; Lambertsen and Duffield 1987; Duffield and Chamberlin-Lea 1990). In *Tursiops truncatus*, *Orcinus orca*, and *Megaptera novaeangliae* at least half of the chromosome

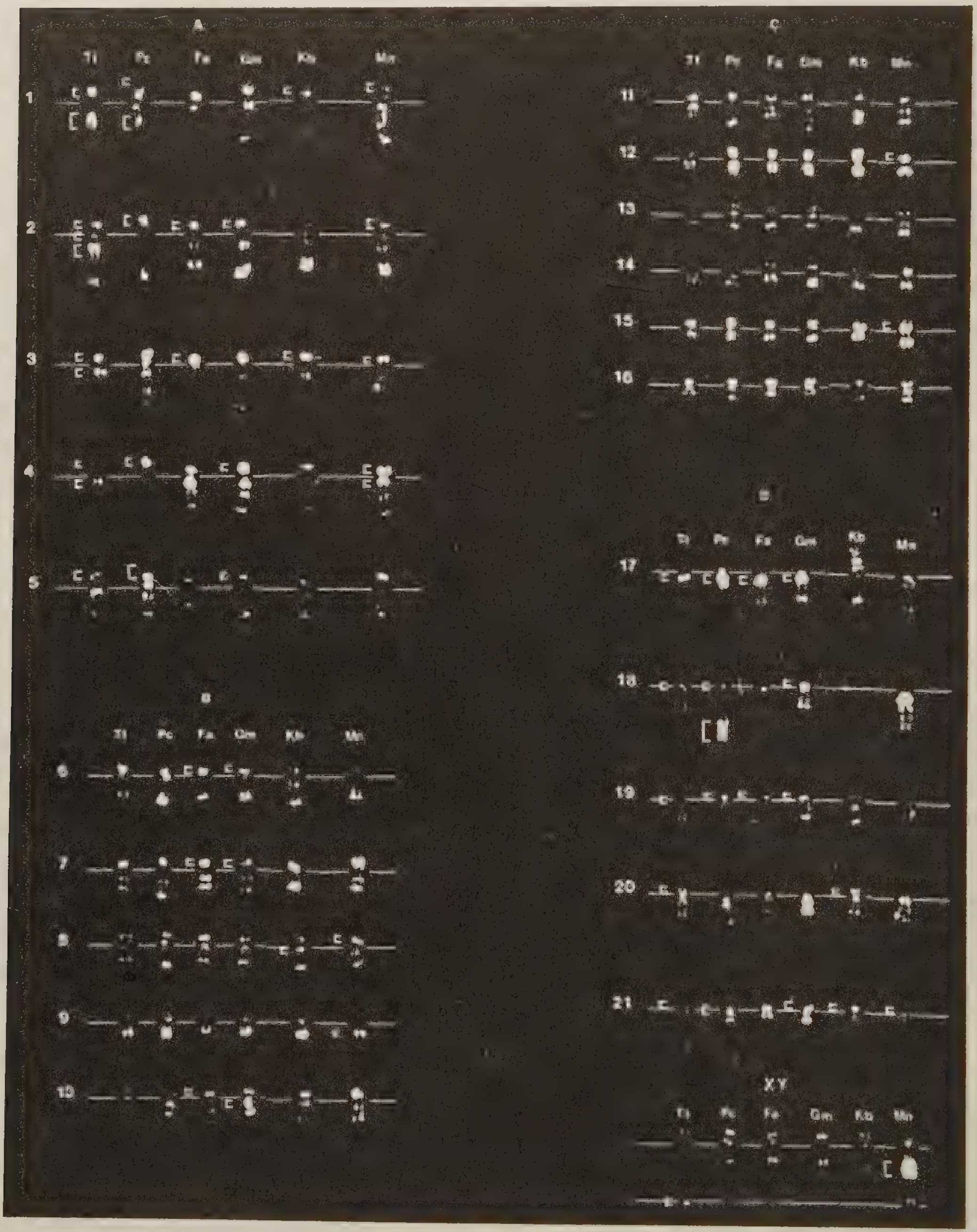
A
Tt Pc Fa Gm Kb Mn
1
2
3
4
5
B
Tt Pc Fa Gm Kb Mn
6
7
8
9
10
C
Tt Pc Fa Gm Kb Mn
11
12
13
14
15
16
D
Tt Pc Fa Gm Kb Mn
17
18
19
20
21
XY
Tt Pc Fa Gm Kb Mn

Figure 6

One chromosome of each chromosome pair from the karyotypes of *Tursiops truncatus* (Tt) compared to those of *Pseudorca crassidens* (Pc), *Feresa attenuata* (Fa), *Globicephala macrorhynchus* (Gm), *Kogia breviceps* (Kb), and *Megaptera novaeangliae* (Mn), to demonstrate the positions of known R-band heteromorphic regions in the chromosomes of these species (brackets). Note the unusual blocks of R-band heteromorphic material in *P. crassidens* (D-18) and in *M. novaeangliae* (X chromosome).

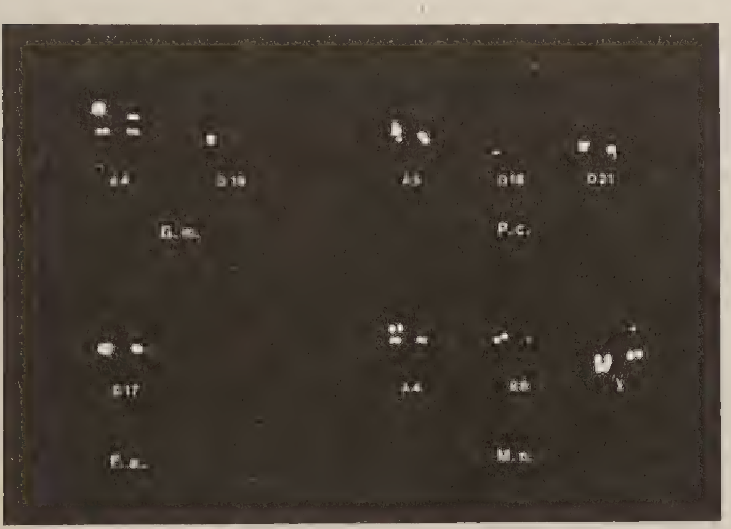

Figure 7
Examples of the types of R-band variants seen in various heteromorphic regions in the karyotypes of *Globicephala macrorhynchus* (Gm), *Pseudorca crassidens* (Pc), *Feresa attenuata* (Fa), and *Megaptera novaeangliae* (Mn).

pairs in their karyotypes exhibit these heteromorphic regions which may vary in size and in intensity of staining.

Chromosome pairs exhibiting R-band heteromorphisms in this study are indicated in each of the karyotypes (Figs. 1–5). A comparison of the distribution of heteromorphic regions in the chromosomes of the five stranded cetacean species and *T. truncatus* (Fig. 6) shows that many of the R-band heteromorphic regions are in the same chromosomal locations in all six species; however, there are also species differences (*see, for example,* the X chromosome in *M. novaeangliae* and D-18 in *P. crassidens*). Examples of the types of heteromorphisms seen in this study are illustrated in Figure 7. In *T. truncatus*, 52 heteromorphisms for 11 chromosome pairs have been found among 104 animals studied (Duffield and Chamberlin-Lea 1990). This number of variants makes R-band heteromorphism analysis extremely useful in population studies, especially when hypotheses of specific relationships need to be tested. As more individuals of each of the stranded species are karyotyped, the number of recognizable heteromorphic regions and the range of heteromorphisms within these regions will be established.

In cetaceans, R-band chromosome heteromorphisms have been used both as genetic markers for determining parentage in captive breeding programs (Duffield et al. 1986; Duffield and Chamberlin-Lea 1990; Hewlett et al. 1989) and for investigating population structure in the field (Lambertsen and Duffield 1987; Duffield and Wells 1988; Duffield et al. 1989). An exciting application of R-band heteromorphisms analysis for stranded cetaceans lies in its potential for confirming suspected relationships among animals stranding together, as in Florida, for example, where *K. breviceps* often strand in adult female-calf pairs or in adult female-calf pairs accompanied by a juvenile or adult male (D. Odell, pers. obs.). Similarly, chromosome heteromorphism analysis could be useful in a mass stranding situation to investigate relationships among specific individuals.

The use of cornea to establish cell cultures from postmortem cetaceans opens up the possibility for cytogenetic studies on stranded cetaceans which have been dead for several days. Fluorescent R-band chromosome heteromorphisms in the karyotypes of these species, as well as the existence of unique marker chromosomes, provide cytogenetic markers for assessing relationships within groups of stranded animals and for looking at regional population differences in these species.

Acknowledgments

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Citations

Arnason, U.
1974. Comparative chromosome studies in Cetacea. Hereditas 77:1–36.
1980. C- and G-banded karyotypes of three delphinids: *Stenella clymene*, *Lagenorhynchus albirostris* and *Phocoena phocoena*. Hereditas 92:179–187.
1981. Banding studies on the gray and sperm whale karyotypes. Hereditas 95:277–281.

Arnason, U., and K. Benirschke.
1973. Karyotypes and idiograms of sperm and pygmy sperm whales. Hereditas 75:67-74.

Arnason, U., K. Benirschke, W.W. Nichols, and J.G. Mead.
1977. Banded karyotypes of three whales: *Mesoplodon europaeus*, *M. carlhubbsi* and *Balaenoptera acutorostrata*. Hereditas 87:189-200.

Arnason, U., R. Lutley, and B. Sandholt.
1980. Banding studies on six killer whales: an account of C-band polymorphism and G-band patterns. Cytogenet. Cell Genet. 28:71-78.

Arnason, U., H. Bellamy, P. Eyporsson, R. Lutley, J. Sigurjonsson, and B. Widegren.
1985. Conventionally stained and C-banded karyotypes of a female blue whale. Hereditas 102:251-253.

Benirschke, K., and A. Kumamoto.
1978. The chromosomes of Cuvier's beaked whale, *Ziphius cavirostris*. Mammal. Chrom. Newsl. 19:70-72.

Bradbury, E.M., N. Maclean, and H.R. Matthews.
1981. DNA, chromatin and chromosomes. John Wiley & Sons Inc, New York, NY, 281 p.

Conrad, G.W.
1970. Collagen and mucopolysaccharide biosynthesis in mass cultures and clones of chick corneal fibroblasts in vitro. Devel. Biol. 21:611-635.

Dahl, I.W., W. Johnsen, A. Anseth, and H. Prydz.
1974. The synthesis of glycosaminoglycans by corneal stroma cells in culture. Expl. Cell Res. 88:193-197.

Doughman, D.J., D. Van Horn, W.P. Rodman, P. Byrnes, and R.L. Lindstrom.
1976. Human corneal endothelial layer repair during organ culture. Archives Ophthal. 94:1791-1796.

Duffield, D.A.
1977. Phylokaryotypic evaluation of the Cetacea. Ph.D. diss., Univ. California, Los Angeles, 154 p.
1982. Indian River *Tursiops*: genetic studies. *In* Live capture, marking and resighting of bottlenose dolphins, *Tursiops truncatus*. Final Rep. NMFS contract NA80-GA-C-00063, p. 312-324.
1986. *Orcinus orca*: taxonomy and evolution - cytogenetics and population structure. *In* Behavioral biology of killer whales (J. Lockhard and B. Kirkevold, eds.), p. 19-33. Alan R. Liss, New York.

Duffield, D.A., and J. Chamberlin-Lea.
1990. Use of chromosome heteromorphisms and hemoglobins in studies of dolphin populations and paternities. *In* The bottlenose dolphin (S. Leatherwood and R.R. Reeves, eds.), p. 609-620. Acad. Press, San Diego CA.

Duffield, D.A. and R.S. Wells.
1988. New ways of looking at whales: use of molecular techniques in the study of social structure in bottlenose dolphins. *In* The world's whales, a closer look (S. Taylor, ed.), p. 41-50. Am. Cet. Soc., San Pedro, CA.

Duffield, D.A. J. Chamberlin-Lea, R.S. Wells, and M.D. Scott.
1985. Inheritance of an extra chromosome in a resident female band of bottlenose dolphins in Sarasota, Florida. Abstract, 6th Bienn. Conf. on the Biology of Marine Mammals, Vancouver, B.C.

Duffield, D.A., J. Chamberlin-Lea, M.A. Dudley, and L.H. Cornell.
1986. Dolphin chromosome variation: an example of the application of R-band heteromorphism analysis to the discrimination of paternity. Abstract, 17th Ann. Conf. Intern. Assoc. Aquatic Animal Medicine, Biloxi, MS.

Duffield, D.A., R.S. Wells, J. Chamberlin-Lea, P.L. Goldie, A.B. Irvine, and M.G. Scott.
1989. The genealogy of a bottlenose dolphin community. Abstract, 8th Biennial Conf. on the Biology of Mar. Mammals, Pacific Grove, CA.

Hack, M.S., and H.J. Lawce (editors).
1980. Association of Cytogenetic Technologists Cytogenetics Laboratory Manual. Assoc. of Cytogenet. Tech., 677-S, Univ. Calif., San Francisco, 430 p.

Hewlett, K.G., J. Chamberlin-Lea, P.L. Goldie, D.A. Duffield, and T.A. Stevens.
1989. Determination of paternity in killer whales (*Orcinus orca*) by chromosomes and DNA fingerprinting. Abstract, 8th Biennial Conf. on the Biology of Mar. Mammals, Pacific Grove, CA.

Irvine, A.B., M.D. Scott, R.S. Wells, and J.H. Kaufmann.
1981. Movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Florida. Fish. Bull., U.S. 79: 671-688.

Kenney, M.C., L.M. Shih, U. Labermeir, and D. Satterfield.
1986. Modulation of rabbit keratocyte production of collagen, sulfated glycosaminoglycans and fibronectin by retinol and retinoic acid. Biochem. Biophys. Acta 889:156-162.

Lambertsen, R.H., C.S. Baker, D.A. Duffield, and J. Chamberlin-Lea.
1988. Cytogenetic determination of gender among individually identified humpback whales (*Megaptera novaeangliae*). Can. J. Zool. 66:1243-1248.

Lambertsen, R.H., and D.A. Duffield.
1987. Biopsy studies of the humpback whale, *Megaptera novaeangliae*. NMFS and Int. Whaling Comm. Tech. Rep. 50-EANF-5-00094, 72 p.

Leeson, T.S., and C.R. Leeson.
1981. Histology. W.B. Saunders Co., Philadelphia, PA, 4th ed. 600 p.

Manski, W., and T.L. Whiteside.
1974. Cell-surface receptors of normal regenerating and cultured corneal epithelial and endothelial cells. Invest. Ophthalmol. 13:935-955.

Pimenova, M.N., and V.D. Simonenko.
1974. Metod kul'tivirovaniia rogovitsky glaza myshi in vitro. Tsitologiya 16:1179-1181.

Sahar, E., and S.A. Latt.
1978. Enhancement of banding patterns in human metaphase chromosomes by energy transfer. PNAS 75(11):5650-5654.

Schweizer, D.
1980. Simultaneous fluorescent staining of R-bands and specific heterochromatic regions (DA-DAPI) bands in human chromosomes. Cytog. Cell Genet. 27:190-193.

Stock, A.D.
1981. Chromosomal variation and constitutive heterochromatin in three porpoise species (genus *Stenella*). Cytogenet. Cell Genet. 31:91-100.

Van Horn, D.L., D.D. Sendele, S. Seideman, and P.J. Buco.
1977. Regenerative capacity of the corneal endothelium in rabbit and cat. Invest. Ophthalmol. Visual Sci. 16(7):597-613.

Wells, R.S.
1986. Population structure of bottlenose dolphins: behavioral studies along the central west coast of Florida. NMFS Tech. Rep. 45-WCNF-5-00366.

Wells, R.S., A.B. Irvine, and M.D. Scott.
1980. The social ecology of inshore odontocetes. *In* Cetacean behavior: mechanisms and processes (L.M. Herman, ed.), p. 263-317. Wiley & Sons, NY.

Worthen, G.L.
1981. Preliminary analysis of the potential for stock assessment of Pacific ocean Delphinids by G and C chromosome banding. NMFS Rep. LJ-81-02C, 99 p.

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Reproductive performance of yellowtail rockfish, *Sebastes flavidus*

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Key words: Reproduction, Sex ratio, Maturity, Fecundity, Gonadogenesis, Scorpaenidae

Synopsis

Field and laboratory studies were conducted for 3 years on the yellowtail rockfish, *Sebastes flavidus*, from Cordell Bank, California, in order to characterize the reproduction of this species whose northern stocks have declined. Research findings included reversal of the sex ratios and male-female ages and sizes at age throughout the annual cycle, heavier and longer females at age than males after sexual maturation, maturation of females at 6 and males at 8 years, long reproductive lifespans, distinct male and female gonadosomatic index patterns over the annual cycle, age- and size-specific fecundity, no difference between potential and realized fecundity and the seasonal changes associated with gonadogenesis. The reproductive profile of the Cordell Bank yellowtail rockfish provided a base for comparison with northern populations that appeared to differ, especially in age and size.

Introduction

In this study the reproduction of yellowtail rockfish, *Sebastes flavidus*, is thought of as a complex of observable, measurable performances. These traits continuously and dynamically change or adapt in time and space at multiple levels of organization from the community to tissue levels in response to environmental conditions, including exploitation. This expands on Lewontin's (1958) concept that populations adapt in two ways: through intergenerational genetic variability and through individual phenotype plasticity. Since no single trait or property can accurately represent the adaptive or reproductive capacities of individual fish, populations or species, we used a multidimensional research approach to understand reproduction and its role in population persistence.

To examine the functional relationships between yellowtail rockfish and their environments, a physiological ecology research program was initiated in 1985. The research goal was to identify, describe and understand the factors that determine yellowtail rockfish condition and reproduction for use in assessing health of the stock and ultimately forecasting recruitment in the population. This paper describes reproductive performance and characterizes a yellowtail rockfish population from a California coastal seamount.

Materials and methods

Subadult and adult yellowtail rockfish were collected from April 1985 to April 1988 from Cordell Bank, California. Fish that had immature, nonfunctional gonads were classified as subadults. Monthly cruises provided 1418 specimens caught by hook and line; of these 487 (390 females and 97 males) were randomly subsampled for further de-

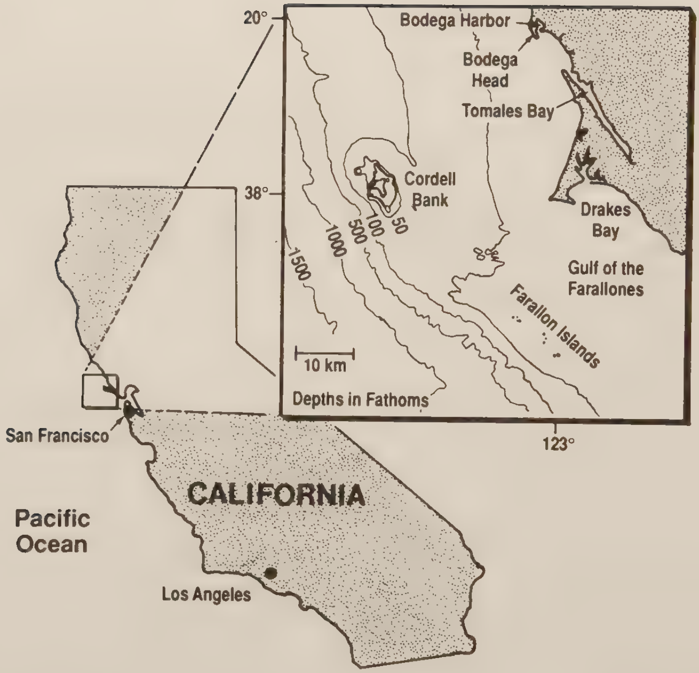

Fig. 1. Cordell Bank, California, site of study on reproduction of yellowtail rockfish.

tailed analysis. All fish collected during these monthly cruises were identified and enumerated. An additional total of 168 trawl-caught yellowtail rockfish females were sampled from the commercial catch from November to March of each year for studies relating to maturity and fecundity. Cordell Bank is the northernmost seamount (38°01'N, 123°25'W) of the California continental shelf (Fig. 1). The bank lies approximately 372 km west of the California coast and covers 62 km of seafloor within the 91 m depth contour. The highest elevation on the bank is 35 m below the sea surface. A total of 22 adult yellowtail rockfish were captured on the bank in November and December of each year and transported, after air bladder deflation, to 2200 l tanks in the laboratory. Fish were held in the laboratory throughout the normal maturation period and allowed to complete parturition, being maintained under ambient photoperiod and water conditions and fed fresh fish ad libitum. All fish were weighed and measured, and 11 were sacrificed for internal examination of gonadal state after parturition or the normal parturition period.

Fish were examined in the laboratory within 24 h of capture, to assess their physiological conditions and reproductive states. Comprehensive examination protocols included morphometrics (length, breadth, width), gravimetrics (total weight, visceral weight, gonad weight, liver weight) and meristics; external and internal examinations of organs for condition (pathologies, fat content, general appearance), diseases and parasites; subsampling of muscle, liver and gonads for proximate analyses, histology and fecundity; and age determination by the otolith break-and-burn method. Fecundity was gravimetrically estimated in triplicate after Gilson fluid fixation. For histology, ovaries were fixed in 10% buffered formaldehyde, dehydrated in ethanol, cleared in xylene and embedded in paraffin (Humason 1967). Testes were fixed in 2.5% glutaraldehyde, postfixed in 1% osmium tetroxide and embedded in epoxy resin (Spurr 1969). Tissues

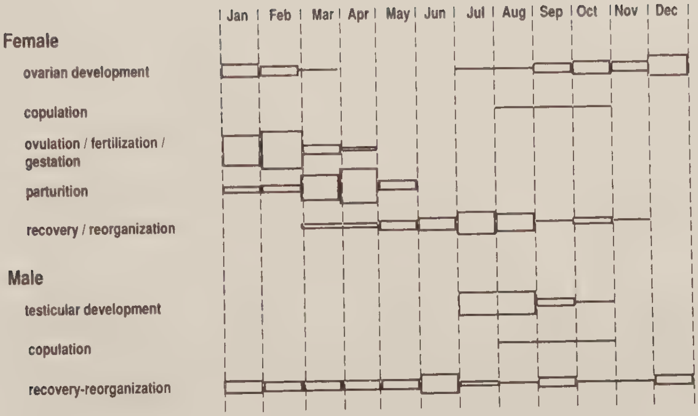

Fig. 2. Annual reproductive performance of male and female yellowtail rockfish from Cordell Bank, California.

were sectioned at 6 μm and stained in hematoxylin and eosin.

Specimen-specific data were managed by using dBASE III +. Subsets were created for individual or group analyses depending on the subtask objectives. Statistical analyses included univariate descriptions, curve fitting, correlation and regression analyses, analysis of variance (ANOVA), analysis of covarience (ANACOV) and graphics, completed with the assistance of Number Cruncher Statistical System 5.01 for microcomputers.

Results

Reproductive performance

The annual sequence of reproductive performance in yellowtail rockfish from Cordell Bank (Fig. 2) followed general patterns described in other studies for many *Sebastes* spp. (DeLacy et al. 1964, Moser 1967, Ni & Templeman 1985, Wyllie Echeverria 1987). Both sexes shared common characteristics of gonadal development, namely a copulation period and a recovery-reorganization period. However, their seasonal patterns differed, and females underwent additional elaboration with the ovulation to parturition developmental sequence that is unique to *Sebastes*.

Ovarian development began just prior to the copulation period and accelerated in September. From October through January, 75% of those females with progressively developing ovaries were observed. Most (89%) that had ovulated and were carrying developing embryos were collected in January and February, and parturition usually occurred in March and April (73%). The prolonged (9 months, March through November) recovery-reorganization period came next and was most obvious just prior to the onset of ovarian development. Male testicular development was rapid, occurring largely during July and August (67%), then declining rapidly with the ending of the copulation period in October. A varying portion of the population appeared in the recovery-reorganization state throughout the year.

Community-population performance

At Cordell Bank the fish community associated with yellowtail rockfish and available to hook and line consisted of 21 species, dominated numerically by yellowtail rockfish (41.5%) followed by *S. rosaceus* (13.9%), *S. paucispinis* (11.3%), *S. chlorostictus* (10.3%), *S. pinniger* (6.2%) and *Ophiodon elongatus* (4.7%). *Sebastes* spp. comprised 94.4% of the total catch. The mean number of species did not seasonally vary (Table 1), nor did the species composition. Catches also were not seasonally dif-

Table 1. Yellowtail rockfish sex ratio (males:females), total yellowtail catch, catch per unit effort (CPUE; No. of fish fisherman^{-1} h^{-1}) and number of total fish species collected on yellowtail rockfish cruises.

	Jan	Feb	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec	xj ± SE
Sex ratio M:F	0.63	1.03	1.65	1.45	1.33	1.62	1.11	0.96	0.41	0.43	0.64	0.43	0.97 ± 0.47
Yellowtail catch	175	117	206	108	41	145	136	98	49	99	82	162	118.2 ± 49.4
CPUE	3.19	2.53	3.44	1.63	1.68	3.78	2.80	3.54	1.83	2.31	2.09	2.02	2.57 ± 0.76
No. of species	11	9	8	10	8	11	9	9	10	9	11	11	9.7 ± 1.2

ferent; mean monthly catch per unit effort (CPUE) was 2.57. The yellowtail rockfish sex ratios changed throughout the year, despite an even (0.97) mean value for the year. The male to female ratio was approximately even in February and then again in July and August, the main copulation period. Females predominated in September – January and males in March – June.

The male and female subadult yellowtail rockfish were similar in ages and size (Table 2), whereas adult females were heavier and longer than males despite identical mean ages of 17.2 years. The seasonal distribution of these parameters (Fig. 3) indicated that males were generally older than females during March – May and were younger in other months. Females on average were longer and heavier in all months except March, and their average size greatly increased after June while that of males slightly decreased. True sexual dimorphism was apparent (Fig. 4). Body depths at length were not significantly different (ANACOV, $p \geq 0.05$) between males and females, but age-specific total wet weights and standard lengths diverged significantly (ANACOV, $p \leq 0.05$) in fish older than 8 years of age. Males also exhibited a narrower range of ages than did females (5–39 versus 4–45 years). All reproductive processes from ovulation and fertilization through parturition occurred from January through May (Fig. 2). The highest incidence of females with newly fertilized eggs and eyed embryos was found in January and February (Table 3), and spent fish were most frequent after February. It appeared that older fish spawned early in the season. Mean ages of females with either fertilized eggs, eyed embryos or newly spent ovaries were higher than those in succeeding months.

Individual performance

Individual reproduction was best monitored in the laboratory. Maturation and spawning of experi-

Table 2. Means, standard deviation and range of ages (year; Rg), total wet weight (g) and standard length (cm) of subadult and adult male and female yellowtail rockfish.

	Age			Total wet weight			Standard length		
	$\bar{x}$	SD	Rg	$\bar{x}$	SD	Rg	$\bar{x}$	SD	Rg
Subadults									
Male (n = 18)	7.2	2.0	5–11	710.1	212.1	425–1244	29.6	2.7	25.35
Female (n = 23)	6.7	1.5	4–10	722.9	315.5	362–1879	28.7	3.1	23–36
Adults									
Male (n = 79)	17.2	7.1	6–39	1156.2	209.0	669–1660	36.1	2.1	32–42
Female (n = 317)	17.2	7.2	6–45	1462.4	396.0	590–2693	38.9	3.7	29–49

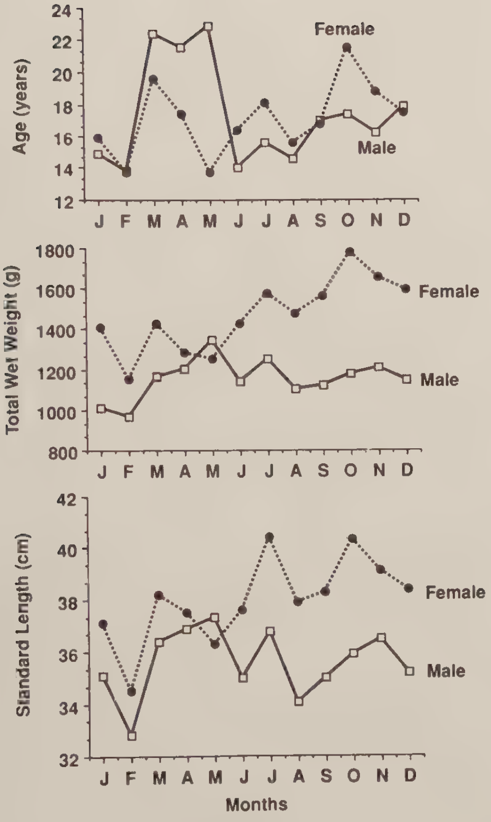

Fig. 3. Mean monthly age (years), total wet weight (g) and standard length (cm) of yellowtail rockfish from Cordell Bank, California.

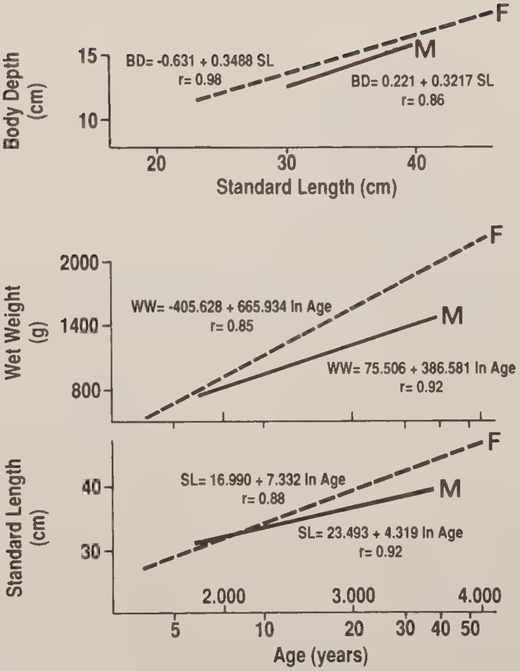

Fig. 4. Linear regression plots of standard length, wet weight by age and body depth by standard length of male (n = 97) and female (n = 340) yellowtail rockfish from Cordell Bank, California.

mental fish held in the laboratory were similar to those in field-caught specimens. Seven of 22 laboratory fish with a mean age of 24 years completed maturation and released embryos. Fish that did not successfully spawn had a mean age of 9.5 years. Examination of these fish showed that they ceased ovarian development and resorbed their eggs. All seven females ceased feeding 3–5 days before parturition, and fish became reclusive and had high opercular ventilation rates. All releases occurred during the night. Examination of fish within 2–5 days after parturition showed that extrusion of embryos was nearly complete and that ovaries quickly began recovery and reorganization with the firming of tissues and reduction of the lumen and ovarian flaccidity.

Ages at maturity were estimated by contrasting individual subadults with undeveloped gonads with adults with gonads in late stages of development (Table 4). Males tended to be slightly, but not significantly (t-test, $p \geqslant 0.05$), older than females. Adults that appeared mature by having gonads in advanced stages of maturation and adults that had fully developed ova, fertilized eggs or spent ovaries did not differ significantly in age (t-test, $p \geqslant 0.05$), and they had broad age ranges (8–39 years for males; 6–45 years for females) and wide distributions (coefficients of variation, 36.2 – 39.8%).

By subtracting the minimum ages at maturity from the age frequencies of the males and females, we were able to plot the average distributions of reproductive lifespans within the male and female yellowtail rockfish stock (Fig. 5). Age distributions

Table 3. Percent composition and adult mean ages, by month, of adult yellowtail rockfish with fertilized eggs, eyed embryos or spent ovaries.

Reproductive state	Month	N	% of total	Adult mean age (years)
Fertilized eggs	Jan	13	39	21.2
	Feb	17	52	15.8
	Mar	3	9	18.3
Eyed embryos	Jan	2	66	26.0
	Feb	1	33	9.0
Spent ovaries	Jan	3	4	28.0
	Feb	5	6	26.0
	Mar	25	32	20.7
	Apr	32	41	19.4
	May	10	13	15.7
	Jun	6	8	13.7

and reproductive lifespans of males and females were polymodal. Potential reproductive lifespans were high, 31 years (range 8–39 years) for males and 39 years (range 6–45 years) for females. The mean reproductive lifespans were the same – 11 years (shaded area) for males (8–19 years) and females (6–17 years). Based on the age composition of the stock, 55% of the males and 59% of the females had reproductive lifespans of 0–11 years.

Whole body changes occurred with gonadal development, especially in females. Females increased in breadth and width as ovaries enlarged. Both sexes had seasonally enlarged urogenital papillae, males during the copulatory period and females during parturition.

Organ performance

The most easily quantifiable trait reflecting seasonal gonadal changes was the gonadosomatic index (GSI = gonad wet weight in grams (total body wet weight in grams)$^{-1}$ × 100). The low subadult GSI's and absolute gonad weights easily separated subadults from mature adults during the gonadal developmental period. Mean GSI value for adult males was 0.257 versus 0.098 for subadults; mean GSI value for adult females was 3.22 versus 0.486 for subadults. Seasonal GSI patterns for adults were distinctive (Fig. 6). Male GSI's remained low from January to June, were highest during testicular development and the copulation period and peaked in August. The GSI's of females were cyclic, but the increase in GSI's with gonadal development was more gradual, with a distinct peak in January and a graduated but rapid decline during early recovery.

Estimated fecundity by fish length, age or weight showed no significant difference among the 3 years (ANOVA, $p \geq 0.01$; Fig. 7). The highest correlations were seen between fecundity and total body wet weight. A comparison of age-specific fecundity in pre-fertilized and fertilized fish indicated that there was no significant difference (ANOCOV,

Table 4. Age and standard length (SL) of male and female of yellowtail rockfish in all reproductive states, and comfirmed mature adults (those with fully mature or recently spent gonads). Rg = range.

	Male			Female		
	x̄	SD	Rg	x̄	SD	Rg
Subadults						
Age (years)	7.2	2.0	5–11	6.7	1.5	4–10
SL (cm)	29.6	2.7	25–35	28.7	3.1	23–36
All adults						
Age	17.2	7.1	6–39	17.2	7.2	6–45
SL	36.1	2.1	32–42	38.9	3.7	29–46
Confirmed adults						
Age	19.5	6.7	8–39	17.6	7.0	6–45
SL	36.6	2.7	32–42	37.6	3.7	29–46.0

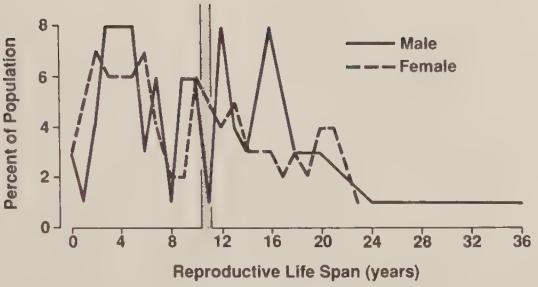

Fig. 5. Distribution, in percent of the population, of reproductive lifespans of male and female yellowtail rockfish from Cordell Bank, California. Shaded area represents mean reproductive lifespan for males and females.

$p \geq 0.05$) between potential and real fecundity (Fig. 8).

Annual sequences of macroscopic gonadal changes were apparent. Most male subadult testes appeared small, translucent, elongated structures, triangular in cross section to threadlike. Colors ranged from translucent pink to yellowish white. With maturity, testes enlarged and became firm and triangular. The pink changed gradually to all white, the process beginning as a white line along the sperm duct. During the peak of the copulation period, testes contained free-flowing sperm. Associated with this ripened condition were large urinary bladders usually full of urine; the urogenital papillae were enlarged and distended. After the copulation period, testes gradually lost their white appearance, beginning at the periphery. Testes slowly became light brown to pink-gray and decreased in size.

Young, immature females had paired, translucent, ribbonlike ovaries ventral to the swim bladder. With the onset of maturity during the developmental period, ovaries enlarged and were circular. Ovaries changed from pale pink to yellowish orange as yolk accumulation progressed. No black pigmentation spots were visible. This process was reversed during the recovery-reorganization period.

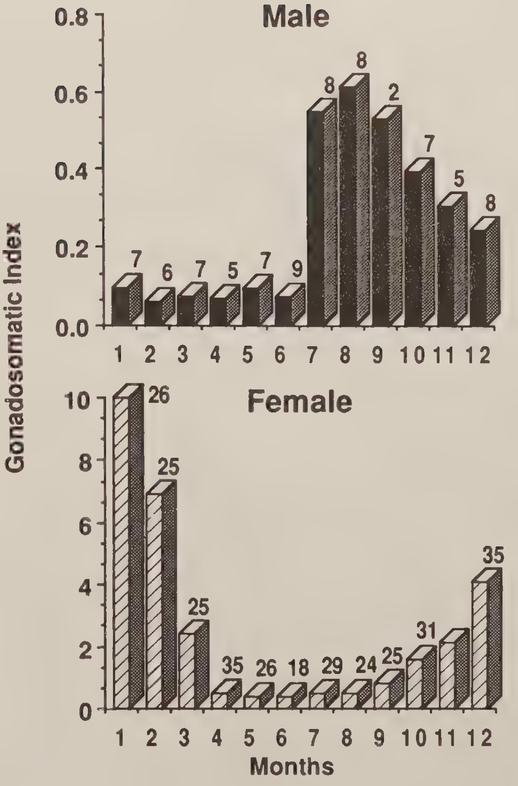

Fig. 6. Mean monthly gonadosomatic index [gonad wet weight in grams (g) (total body wet weight (g))$^{-1} \times 100$] of male and female yellowtail rockfish from Cordell Bank, California.

Ovaries in mature females underwent notable seasonal changes. After the copulation period, ovaries began to enlarge and to change from a pale pink to yellow-orange. Ovaries gradually enlarged to occupy over half the peritoneal cavity volume. As the time of ovulation approached, the large eggs could be easily teased from their clustered follicles. At ovulation and fertilization, eggs dramatically increased in clarity and became more yellowish blue. The thin ovarian walls encased ovaries turgid with free eggs. As gestation proceeded, the ovaries assumed a gray-green appearance largely due to the pigmentation of embryonic eyes.

After parturition, which probably occurred over a period of hours based on laboratory observations, the ovaries appeared as flaccid sacks with vacuous lumens. Residual embryos were occasionally visible in the lumen. Ovaries appeared dark red-brown at this stages. Recovery and reorganization occurred rapidly within a few days. Flac-

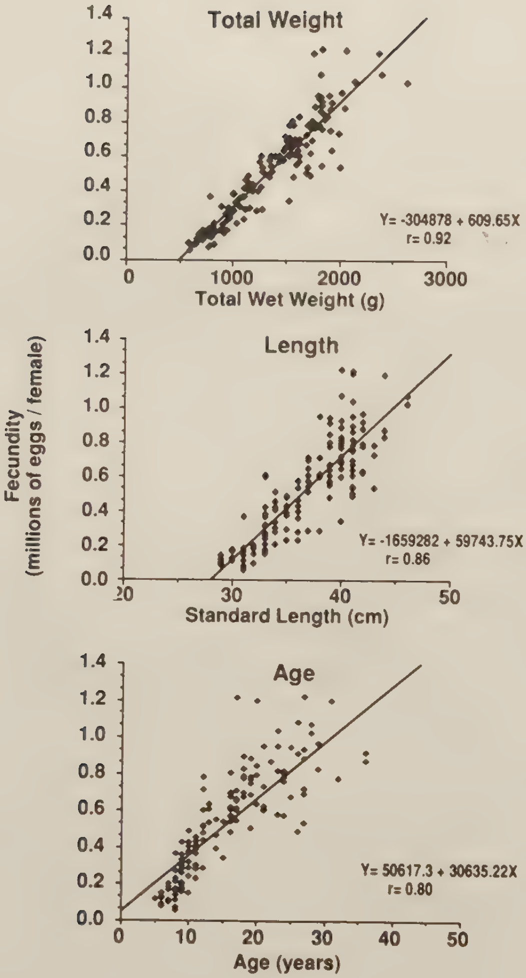

Fig. 7. Fecundity by total weight, standard length and age of yellowtail rockfish from Cordell Bank, California.

cidity decreased, lumens decreased, walls thickened, and colors changed to brown-pink. Often randomly placed, small, black spots were visible, especially along the ventral midline.

Tissue performance

Histological examination confirmed that yellowtail rockfish were determinate spawners. At this level of organization, it was possible to closely monitor the annual reproductive cycle. This definitive examination served as a sensitive measure of the yellowtail rockfish's reproductive state.

Elongate testes had an unrestricted, tubular-type structure throughout (Grier 1981). Efferent seminiferous tubules branched off the central sperm ducts and became increasingly smaller towards the periphery. Intratubular spaces contained germinal epithelium composed of Sertoli cells and spermatogenic germ cells (cysts). Extratubular spaces were the site of Leydig cells, usually found in conjunction with capillaries, nerves, smooth muscle and fibroid cells, all in a connective tissue matrix, the stroma. Testes were bordered by squamous epithelium. Spermatogenesis occurred in cysts, progressing from the periphery to the sperm ducts. Early in testicular recrudescence, tubules contained cysts of primary and secondary spermatogonia, widely separated by Sertoli cells. Mitotic and meiotic divisions of secondary spermatogonia led to formation of spermatocytes, close apposition of cysts and crowding of tubules. As maturation proceeded, spermatogonia throughout the testes appeared tightly packed within the cysts. The developmental progression from spermatid to spermatozoan formation occurred within the cysts, which then burst and released spermatozoa into tubules. In these final stages, mature spermatozoa were found throughout collecting tubules and ducts. During the post-copulation period, gradual recovery and reorganization were observed wherein residual sperm and cytoplasm in the lumens, and the ducts were resorbed by Sertoli cells. Peripheral areas showed reformation of the cysts and the presence of primary and secondary spermatogonia. Immature testes also contained these initial spermatogonia. They differed from mature testes in that cysts were small along with tubular lumens, and they showed no evidence of residual spermatozoa.

Paired ovoid ovaries consisted of stroma and oogonial nests that underwent acinar development along margins of lamellar branches throughout the ovaries. The stroma-germ tissue complex was encased in a thin ovarian wall of squamous epithelium and smooth muscle that seasonally varied in thickness.

A seasonal developmental progression of follicle

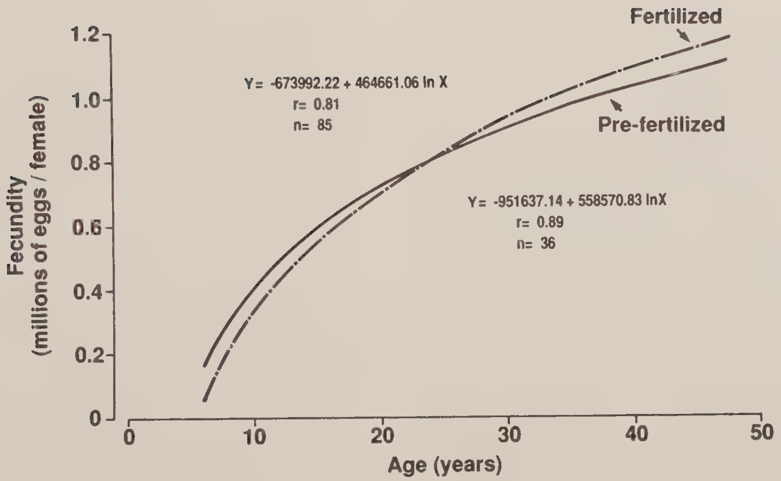

Fig. 8. Semilogarithmic plot of fecundities of yellowtail rockfish with pre-fertilized and fertilized eggs by age.

and oocyte growth was observed. Differentiation was accompanied by increased vascularization and movement of epithelial cells towards the surface of the oocytes. Small (5–25 μm) nested oogonia with transparent cytoplasm, dark-stained nuclei and larger (20–100 μm) early peri-nucleolus oocytes were found in ovarian tissues year-round. These were considered undeveloped or 'resting' stage oocytes (Bowers & Holliday 1961, Howell 1983). With the onset of recovery and reorganization, oocytes (ca. 50–140 μm diameter)—with numerous, randomly distributed, clear lipid vacuoles, increasingly large nuclei and peripherally arranged nucleoli—increased in frequency. By mid to late summer, cytoplasmic granulated yolk accumulated as oocytes enlarged (120–210 μm). With increasing ovarian development, over half the interior of these oocytes became filled with large yolk globules, and lipid vacuoles coalesced and enlarged. In the final developmental stages, the large (600–750 μm) oocytes contained single, large lipid vacuoles and amoeboid nuclei. With ovulation, follicle components disintegrated while the capillary network was maintained and remained in close association with the egg. Embryos were observed as free from lamellae in the ovarian lumen. Spent ovaries quickly recovered and histologically displayed increased vascularization, with empty or collapsed follicles in various resorptive stages. Occasional residual embryos and unfertilized oocytes were seen in various stages of degeneration. As ovaries reorganized, lamellar branches and associated stroma became compact and firm, and small nested oocytes as first described became most numerous. Ovaries of immature fish contained early developing oocytes, and there was no evidence of yolk accumulation nor recovering resorptive tissues.

Discussion

The Cordell Bank yellowtail rockfish population's annual sex ratio reversal showed a pattern not previously observed in rockfishes. A coastwide study of yellowtail rockfish (Fraidenburg 1980) showed males dominated (56–74%) in each area with no latitudinal trend. This survey was conducted during mid to late summer, the transition period in our study when the sex ratio changed from male dominance to even ratios and then to predominantly females. Northwest Atlantic studies (Ni & Sandeman 1984, Ni & Templeman 1985) of three *Sebastes* species noted, as in our study, an overall even sex ratio for the year, but females were more abundant for all but 3 months (March, June and August). These species were behaviorally different in that the sexes were believed to segregate in different seasons. Yellowtail rockfish are believed to be nonmigratory and to remain close to areas that they colonize as juveniles (Carlson & Haight 1972, Calson 1986). Changes in sex ratios may have resulted from differences in feeding behavior or localized sex segregation. It is also possible that male aggression associated with territoriality, as noted by Shinomiya & Ezaki (1991), could account for more males being caught by hook and line.

The age and size composition of the Cordell Bank population appeared different from those of northern populations. This is important because the composition determines the reproductive capacity of the population. The coastwide rockfish survey of Fraidenburg (1980) showed a north to south cline of decreasing age and size. Since that study, a decade of monitoring of the commercial catches in Oregon and Washington has provided evidence of significant declines in mean ages and sizes (Tagart 1988). Preliminary results of our own field studies on Washington yellowtail rockfish support these findings (National Marine Fisheries Service, Tiburon Laboratory, unpublished data). Northern populations appeared younger overall but were larger than fish of similar ages from Cordell. For example, the mean age of females in northern populations was 12.1 years (versus 17.2 cm for Cordell Bank fish), and mean standard length was 46.6 cm (versus 38.9 cm).

A consistent trend among yellowtail rockfish populations was sexual dimorphism. Females were longer and heavier at age than males. Wyllie Echeverria (1986) provided details on this dimorphism in four *Sebastes* species, including yellowtail rockfish. As noted by Westrheim & Harling (1975), this dimorphism became apparent after fish reached 6–8 years of age (Fig. 4), the approximate ages that we found yellowtail rockfish to mature.

Sebastes usually have a protracted spawning season (Leaman 1988). The parturition period for Cordell Bank yellowtail rockfish occurred from January through May and peaked during March and April (Fig. 2). In the geographically larger study of Wyllie Echeverria (1987), yellowtail rockfish exhibited a similar seasonal pattern. One of our findings is relevant to management: the older fish spawned during the early part of the season. Restricted fishing seasons and selective exploitation in Washington fisheries could affect the reproductive potential of these populations.

Wyllie Echeverria (1987) estimated the ages and sizes at maturity for yellowtail rockfish (males; first = 4 years, 30 cm; 50% = 6 years, 35 cm; 100% = 11 years, 43 cm; females: first = 4 years, 27 cm; 50% = 7 years, 36 cm; 100% = 11 years, 42 cm). Our research design did not allow such precision. Male and female yellowtail rockfish at Cordell Bank were older and larger at first maturity (males: first = 8 years, 32 cm; females: first = 6 years, 29 cm). Our smaller sample size and restricted sampling range could have biased our results. One problem that we are currently trying to resolve is whether the small, young females that appear to have maturing ovaries actually complete the process. Our laboratory observations of these fish and the occurrence of similarly developing fish in the field during the entire developmental period suggest that they remain functionally immature, as has been found in other *Sebastes* species (Westrheim 1958, Leaman 1988).

The duration of the reproductive lifespan is determined by the age at maturity and the life expectancy. Cordell Bank yellowtail rockfish had long potential reproductive lifespans of 31 and 39 years for males and females respectively. The maximum potential span for the species could be 52 years, given an age at maturity of 4 years (Wyllie Echeverria 1987) and a maximum age of 56 (Beamish 1979). Our study estimates over half of the population has real reproductive lifespans of 11 years for both sexes. This trait was largely due to the polymodal, wide-ranging age structure of the population. Fraidenburg's (1980) survey showed this to be a coastwide phenomenon. Long reproductive lifespans have been shown to be important for the persistence of populations in highly variable environments similar to those of the yellowtail rockfish habitats (Stearns 1977).

Fecundity is often used as an index of reproductive effort, and generally it is believed to increase with age (Williams 1966, Gadgil & Bossert 1970). Fecundity of yellowtail rockfish from Cordell Bank correlated well with age and size (Fig. 7). Earlier studies (Phillips 1964, Gunderson et al. 1980) of yellowtail rockfish have found considerably lower fecundity at age and size. These studies may possibly differ because Phillips (1964) presented estimates of fecundity at age based on low precision methods and Gunderson et al. (1980) examined adults over 43 cm using a volumetric subsampling method. Only 2% of our specimens were in that size range. Recent comparisons of methods for estimating fecundity have shown that gravimetric subsampling was more accurate than volumetric subsampling (Leaman 1988). Boehlert et al. (1983) observed decreased fecundity in *Sebastes entomelas* with the approach of parturition. Kusakari (1991) found declining fecundity during gestation in *S. schlegeli*. This suggests that fecundity estimates derived from ovaries in early stages of development do not accurately represent fertility. We found no evidence of this in our study (Fig. 8) although our ongoing histological studies are showing interannual variability in the occurrence of egg resorption. It is possible that our fecundity methodology is not sensitive enough to detect this phenomenon.

Our histological observations proved to be sensitive measures of the reproductive cycle. Structures and apparent functions were similar to those described in other *Sebastes* species (Moser 1967, Lisovenko 1978). They differed in that yellowtail rockfish showed a typical pattern of teleostean group synchronous ovarian development in contrast to the multiple-spawning pattern found in *S. paucispinis*. Histological changes in our yellowtail rockfish ovaries occurred throughout the year, similar to findings in *S. alutus* (Leaman 1988). These changes were easily observed in the cytoplasm, nucleus and follicle, indicating that there is no resting period between reproductive periods. Changes in the male spermatogenic sequence were less dramatic than in that for the females. Recruitment of a season's gametes from a pool of intratubular stem spermatogonia was rapid and of short duration. Wootton (1984) defined life history strategy as the overall pattern shown by an individual. Life history tactics then become the variations in the typical pattern that fish make in response to fluctuations in their environments. With the description and characterization we have provided on the Cordell Bank yellowtail rockfish, we now have the opportunity to expand our studies on spatial, temporal and populational scales to see how other populations have responded and adapted to different habitats. Through knowledge of life history performance, especially reproductive performance, it should be possible to determine the life history adaptive capacity of yellowtail rockfish as a species and to delimit the adaptive capacities of particular populations.

References cited

Beamish, R.J. 1979. New information on the longevity of Pacific ocean perch (*Sebastes alutus*). J. Fish. Res. Board Can. 36: 1395–1400.

Boehlert, G.W., W.H. Barss & P.B. Lamberson. 1983. Fecundity of the widow rockfish (*Sebastes entomelas*) off the coast of Oregon. U.S. Fish. Bull. 80: 881–884.

Bowers, A.B. & F.G.T. Holliday. 1961. Histological changes in the gonad associated with the reproductive cycle of the herring (*Clupea harengus* L.). Department of Agriculture and Fisheries Scotland, Marine Research 5: 1–16.

Carlson, H.R. 1986. Restricted year-class structure and recruitment lag within a discrete school of yellowtail rockfish. Trans. Amer. Fish. Soc. 115: 490–492.

Carlson, R.J. & R.E. Haight. 1972. Evidence for home site and homing of adult yellowtail rockfish, *Sebastes flavidus*. J. Fish Res. Board Can. 29: 1011–1014.

DeLacy, A.C., C.R. Hitz & R.L. Dryfoos. 1964. Maturation, gestation, and birth of rockfish (*Sebastodes*) from Washington and adjacent waters. Washington Department of Fisheries, Research Paper 2: 51–67.

Fraidenburg, M.E. 1980. Yellowtail rockfish, *Sebastes flavidus*, length and age composition off California, Oregon, and Washington in 1977. Mar. Fish. Rev. 42: 54–56.

Gadgil, M. & W.H. Bossert. 1970. Life history consequences of natural selection. Amer. Nat. 102: 52–64.

Grier, H.J. 1981. Cellular organization of the testis and spermatogenesis in fishes. Amer. Zool. 21: 345–357.

Gunderson, D.R., P. Callahan & B. Goiney. 1980. Maturation and fecundity of four species of *Sebastes*. Mar. Fish Rev. 42: 74–79.

Howell, W.H. 1983. Seasonal changes in the ovaries of adult yellowtail flounder, *Limanda ferrunginea*. U.S. Fish. Bull. 81: 341–355.

Humason, G.H. 1967. Animal tissue techniques, 3rd. edition. W. H. Freeman, San Francisco. 641 pp.

Kusakari, M. 1991. Mariculture of kurosoi, *Sebastes schlegeli*. Env. Biol. Fish. 30: 245–251.

Leaman, B.M. 1988. Reproductive and population biology of

Pacific ocean perch (*Sebastes alutus* (Gilbert)). Ph.D. Thesis, University of British Columbia, Vancouver. 200 pp.

Lewontin, R.C. 1958. The adaptations of populations of varying environments. Cold Spring Harbor Symp. Quant. Biol. 22: 395–408.

Lisovenko, L.A. 1978. Reproduction of rockfishes (family Scorpaenidae) off the Pacific coast of South America. J. Ichthyology 18: 262–268.

Moser, H.G. 1967. Seasonal histological changes in the gonads of *Sebastes paucispinis* (Ayres), an ovoviviparous teleost (family Scorpaenidae). J. Morph. 123: 329–351.

Ni, I-H. & E.J. Sandeman. 1984. Size at maturity for Northwest Atlantic redfishes (*Sebastes*). Can. J. Fish. Aquat. Sci. 41: 1753–1762.

Ni, I-H. & W. Templeman. 1985. Reproductive cycles of redfishes (*Sebastes*) from southern Newfoundland waters. J. Northw. Atl. Fish. Sci. 6: 57–63.

Phillips, J.B. 1964. Life history studies on ten species of rockfish (genus *Sebastodes*). Cal. Dep. Fish and Game, Fish Bull. 126. 70 pp.

Shinomiya, A. & O. Ezaki. 1991. Mating habits of the rockfish *Sebastes inermis*. Env. Biol. Fish. 30: 15–22.

Spurr, A.R. 1969. A low viscosity epoxy resin embedding medium for electron microscopy. J. Ultra. Res. 26: 31–43.

Stearns, S.C. 1977. The evolution of life history traits: a critique of theory and a review of the data. Ann. Rev. Ecol. Syst. 8: 145–171.

Tagart, J.V. 1988. Status of yellowtail rockfish stocks in the International North Pacific Fishery Commission Vancouver and Columbia areas. Wash. Dep. of Fisheries, Spec. Report. 114 pp.

Westrheim, S.J. 1958. On the biology of Pacific ocean perch, *Sebastes alutus* (Gilbert). M.Sc. Thesis, University of Washington, Seattle. 106 pp.

Westrheim, S.J. & W.R. Harling. 1975. Age-length relationships for 26 scorpaenids in the Northeast Pacific Ocean. Fish. Mar. Serv. Tech. Report 565. 12 pp.

Williams, G.C. 1966. Adaptation and natural selection. Princeton University Press, Princeton. 307 pp.

Wootton, R.J. 1984. Introduction: strategies and tactics in fish reproduction. pp. 1–12 *In:* G.W. Potts & R.J. Wootton (ed.) Fish Reproduction: Strategies and Tactics, Academic Press, London.

Wyllie Echeverria, T. 1986. Sexual dimorphism in four species of rockfish genus *Sebastes* (Scorpaenidae). Env. Biol. Fish. 15: 181–190.

Wyllie Echeverria, T. 1987. Thirty-four species of California rockfishes: maturity and seasonality of reproduction. U.S. Fish. Bull. 85: 229–250.

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Oceanic upwelling and productivity in the eastern tropical Pacific

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Abstract

An oceanographic survey of the eastern tropical Pacific Ocean in August–November 1990 found a productive, nutrient-rich, moderately high-chlorophyll surface layer in two oceanic upwelling regions: the equatorial divergence, especially east of the Galapagos, and the countercurrent divergence out to 105°W, >1,000 km west of the Costa Rica Dome. Although NO_3 is not depleted in upwelling regions, relationships among nutrient concentrations and temperature in 1986–1988 data from the same area show that NO_3 is the the first macronutrient to be depleted in adjacent, less-productive regions. A three-dimensional, two-layer box model of NO_3 flux within and into the euphotic zone gives estimated rates of new production that are ~29% of measured rates of ^{14}C phytoplankton production. Persistence of excess (saturating) NO_3 in the euphotic zone exceeds 1 yr under high-nutrient, low-chlorophyll conditions off the equator where weak upwelling, or downwelling, occurs. These results indicate substantial control or limitation of NO_3 utilization and productivity in nutrient-rich oceanic regions of the eastern tropical Pacific.

The eastern tropical Pacific contains some of the most productive waters of the world ocean. Concern about atmospheric CO_2 increase and the role of the deep ocean as a sink in the global C cycle has presented oceanographers with an important question: what are the rates of new production in large, productive areas of the open ocean and what limits those rates? Nutrients are rarely depleted in surface waters of the equatorial Pacific (Thomas 1979) or in other upwelling regions such as the Costa Rica Dome and coastal Peru and Ecuador. The thermocline is shallow in these regions, so that vertical advection and mixing bring cold, nutrient-rich water from below the thermocline (nutricline) into the surface layer. This nutrient input maintains optimal (saturating) concentrations of NO_3 at the surface and results in relatively high levels of new production (Chavez and Barber 1987), but not high enough to deplete NO_3. Persistence of nutrients at the sea surface characterizes the high-nutrient, low-chlorophyll (HNLC) condition that is the subject of this symposium (*see* Cullen 1991).

Surface currents and water masses of the eastern tropical Pacific are illustrated schematically in Fig. 1. Both coastal upwelling along eastern boundaries and oceanic upwelling along offshore divergences occur in this region. The effects of equatorial upwelling are evident in the equatorial thermocline ridge (Fig. 2) and in the anomalously cool temperature of equatorial surface water. Sverdrup et al. (1942) presented evidence of surface divergence and upwelling at two sites in the equatorial current system: in the South Equatorial Current along the equator, and between the North Equatorial Countercurrent and North Equatorial Current at 10°N. The countercurrent thermocline ridge along 10°N is evidence of upwelling in this countercurrent divergence. However, generally warm temperatures and low concentrations of nutrients suggest that the effects of upwelling do not reach the surface except at the eastern end of the ridge in the Costa Rica Dome. Offshore transport of surface waters and coastal upwelling are driven by equatorward longshore winds along the coasts of Baja California and Peru-Ecuador and by topographically induced offshore winds at several points along the

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Acknowledgments

We thank Stephen Reilly for continued support of this work, and the officers and crew of NOAA Ships *McArthur* and *David Starr Jordan.* John Cullen, David Behringer, and two reviewers provided critical comments.

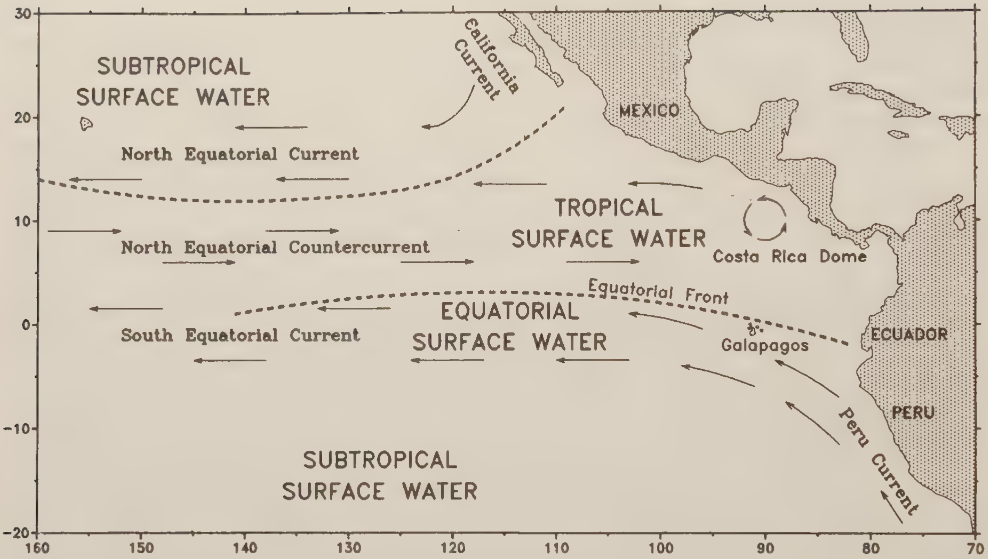

SUBTROPICAL SURFACE WATER
North Equatorial Current
California Current
MEXICO
TROPICAL SURFACE WATER
Costa Rica Dome
North Equatorial Countercurrent
Equatorial Front
EQUATORIAL SURFACE WATER
South Equatorial Current
Galapagos
ECUADOR
PERU
Peru Current
SUBTROPICAL SURFACE WATER
30
20
10
0
-10
-20
160
150
140
130
120
110
100
90
80
70

Fig. 1. Schematic diagram of eastern tropical Pacific surface water masses and surface currents (described by Wyrtki 1967).

coast of Central America (Gulfs of Tehuantepec, Papagayo, and Panama).

Chl and nutrient data have been collected in August–November in the eastern tropical Pacific since 1986 (Fiedler et al. 1992). These data, plus phytoplankton productivity measurements made in 1990, provide an opportunity to examine spatial patterns of nutrient availability and productivity. We examine PO_4-NO_3, SiO_4-NO_3, and NO_3-

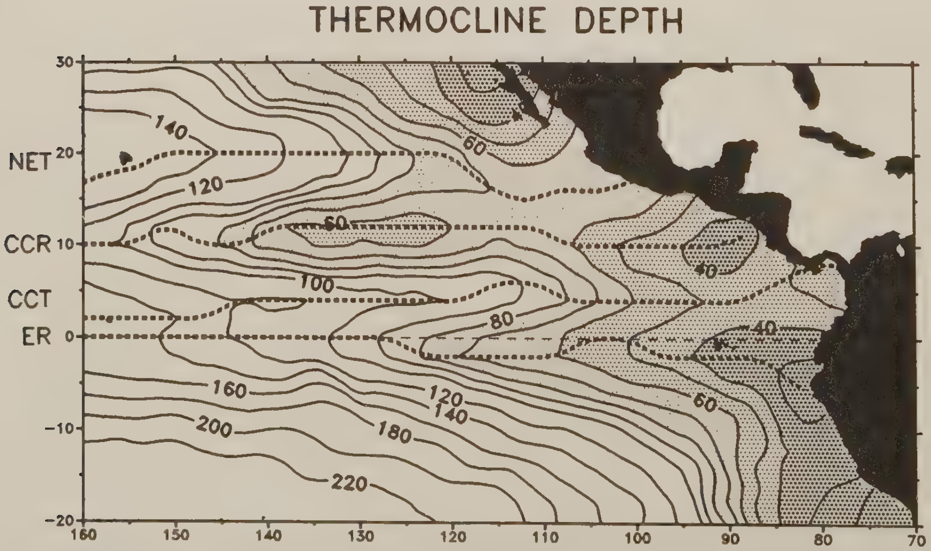

THERMOCLINE DEPTH
NET
CCR
CCT
ER
140
120
60
50
100
80
40
40
60
160
200
120
140
180
220
30
20
10
0
-10
-20
160
150
140
130
120
110
100
90
80
70

Fig. 2. August–November climatology of thermocline (20°C isotherm) depth (Fiedler 1992). ER—Equatorial ridge; CCT—countercurrent trough; CCR—countercurrent ridge; NET—north equatorial trough.

temperature relationships in our large data set to confirm that NO_3 depletion could limit productivity in parts of this region.

Surface current velocities calculated from ship drift reports were used to estimate horizontal transport and divergence within, and upwelling into, the mixed layer. From these rates and our observed NO_3 profiles, we calculated NO_3 fluxes into the euphotic zone and estimated rates of net NO_3 input (new production). New production is thus equal to the rate of NO_3 uptake necessary to maintain the observed NO_3 distribution in a steady state. Past estimates of production based on NO_3 input into the surface layer have used one-dimensional models and ignored horizontal loss or input of unused NO_3 in the euphotic zone (Riley 1956; Sapozhnikov and Galerkin 1973; Chavez and Barber 1987; Jenkins 1988; Yentsch 1990). In contrast, Roemmich (1989) performed a very thorough analysis of mass, heat, and salt balance in the Southern California Bight to derive an estimate of new production from net NO_3 import. Sarmiento et al. (1990) presented a model that estimates new production in the North Atlantic from horizontal and vertical NO_3 balances.

Methods

Field measurements—We collected oceanographic data in a large area of the eastern tropical Pacific (14×10^6 km^2) in August–November of 1986 through 1990. This sampling is part of a National Marine Fisheries Service program to monitor trends in relative abundance of dolphin stocks affected by the yellowfin tuna purse seine fishery. Sampling is constrained by daylight dolphin census operations. We collected XBT profiles, continuous records of surface temperature, salinity and (through 1989) fluorescence, and CTD casts with discrete samples for Chl and nutrient analysis and (in 1990 only) ^{14}C-uptake measurements.

Hydrocasts to 1,000 m were made 2 times per night with a Seabird or Neil-Brown CTD. General Oceanics Niskin bottles (1.7 liters) were retrofitted with silicon rubber O-rings in the valves and endcaps and silicon rubber tubing as the closing mechanism. The bottles were cleaned once a week by washing with a 25% MICRO cleaning solution, rinsing with freshwater, and soaking in 0.25 N HCl for 8 h. Ten rosette-mounted bottles collected water from eight standard depths (0, 20, 40, 60, 80, 100, 125, 150 m) plus two additional standard light depths for phytoplankton productivity casts as described below.

Ten 275-ml subsamples in the morning and eight samples in the evening were collected for phytoplankton pigment analysis. Samples were extracted for 24–36 h with 90% acetone in glass scintillation vials refrigerated in dark boxes. Chl *a* and pheophytin were measured with a Turner Designs model 10-005R fluorometer calibrated with commercial Chl *a* (Sigma). Subsamples (20 ml) were collected from morning productivity casts for nutrient analysis (NO_3, NO_2, PO_4, and SiO_4). These samples were frozen immediately after collection and analyzed later at Monterey Bay Aquarium Research Institute with an Alpkem autoanalyzer.

Water samples for determination of dissolved inorganic C uptake were collected from depths to which 100, 50, 30, 15, 5, 1, and 0.1% of the incident light penetrated. Light depths were estimated from expected euphotic zone depths calculated from pigment profiles observed on previous ETP dolphin surveys (1986–1989) according to Morel (1988). Samples were drawn into aged, "Vitro" glass 150-ml bottles (Wheaton Corp.) rinsed twice with sample water; 10 μCi of $NaH^{14}CO_3$ were added to each sample bottle and the bottles incubated in nickel screens (Perforated Products) in an on-deck seawater-cooled Plexiglas incubator for 24 h with natural sunlight as the light source. The screens act as neutral density filters, reducing the light intensity to the same level as at the depth from which the sample was collected. Two extra samples at the 100 and 0.1% light levels were inoculated with radioactive tracer and filtered immediately with no incubation to determine abiotic particulate ^{14}C incorporation (Chavez and Barber 1987).

For determination of particulate C fixation, the water was filtered onto Whatman GF/F filters at a vacuum of <5.2 cm of Hg, acidified with 0.5 N HCl, and counted in 10 ml of CytoScint ES on a liquid scintillation counter after the 4-month cruise. Total ^{14}C activity was determined by adding 1.0 ml of incubated sample water (from the 100 and 30% light level bottles) to a scintillation vial containing 20 ml of Cytoscint ES cocktail. An average of these two values was used as the total amount of added inorganic C activity in the calculation of C uptake at a station.

Chl and pheopigment profiles measured at 20–25 m intervals were smoothed by cubic spline interpolation. The depth of the Chl maximum was determined from the smoothed Chl profile. Euphotic zone depth (Z_e, 1% PAR level) was calculated from Morel's relationship between Z_e and phytoplankton pigment concentration in the euphotic zone of oceanic case 1 waters, in which phytoplankton play a predominant role in determining optical properties (Morel 1988).

Box model of new production—A two-layer box model was used to calculate NO_3 fluxes into and within the surface layer. The model calculates new production as *the rate of NO_3 uptake necessary to maintain the observed NO_3 distribution in a steady state, given the climatological rates of vertical and horizontal advection derived from ship drift observations.* This new production maintains the steady state NO_3 distribution by loss of organic N from the euphotic zone (export production). Horizontal resolution was 2° × 2° latitude-longitude. The nutrient observations and ship drift data are not dense enough to resolve finer scale variability. New production in a 2° × 2° box was estimated as the net input of NO_3 into the surface layer (euphotic zone) by horizontal and vertical advection. Turbulent mixing from below and secondary sources such as terrestrial runoff and N_2 fixation were not considered, so that the estimates are valid only in upwelling areas and are probably underestimates even there. The model also excludes island effects and topographically induced upwelling that are not resolved by the 2° × 2° grid.

Mean $[NO_3]$ in the euphotic zone (N_e) and $[NO_3]$ at the base of the euphotic zone (N_z) were calculated from our 1986–1988 nutrient data. Euphotic zone depth for each cast was calculated from the phytoplankton pigment profile as described above. The nominal concentration at which uptake of NO_3 by oceanic phytoplankton approaches saturation is taken to be 4 μM (MacIsaac and Dugdale 1969). Thus, excess NO_3 ($N_e - 4.0 > 0$) occurs in the euphotic zone of nutrient-rich waters.

Surface currents were estimated from ship drift data in the National Oceanographic Data Center (NODC) surface current data set. A total of 35,205 ship drift reports in the study area from August to November (1900–1969) were averaged on a 2° × 2°-latitude-longitude grid. Observations were zonally smoothed during gridding by averaging observations within ±2° to 10° longitude of each grid point, so that at least 100 observations are included in each grid mean Fiedler 1992). This procedure ensured sample sizes adequate for estimation of a reliable mean at each grid point, while retaining resolution of the predominantly zonal structure of equatorial surface currents. Mean August–November surface-current vectors are plotted in Fig. 3, which also illustrates the 2° × 2° resolution of the box model.

Mixed-layer depth was estimated as the depth at which temperature is 0.5°C less than surface temperature in 24,928 XBT and MBT profiles collected in the study region in August–November from 1960 through 1989 (Fiedler 1992). The mixed layer defined in this way deepens from east to west and is deeper beneath the equatorial divergence than beneath the countercurrent divergence along 10°N (Fig. 3). This pattern has been observed in other analyses of mixed-layer depth in the eastern tropical Pacific (Wyrtki 1964; Levitus 1982).

Horizontal transports were calculated by assuming that the mean surface currents between boxes, derived from the ship drift data, were uniform through the mixed layer. Vertical transport through the base of the mixed layer was calculated from divergence of the horizontal transports. NO_3 flux was calculated from the product of transport and $[NO_3]$ within or at the base of the euphotic zone. Thus, we assume that the vertical transport calculated at the base of the mixed layer can be applied to the base of the euphotic zone. Euphotic zone depth is 0–30

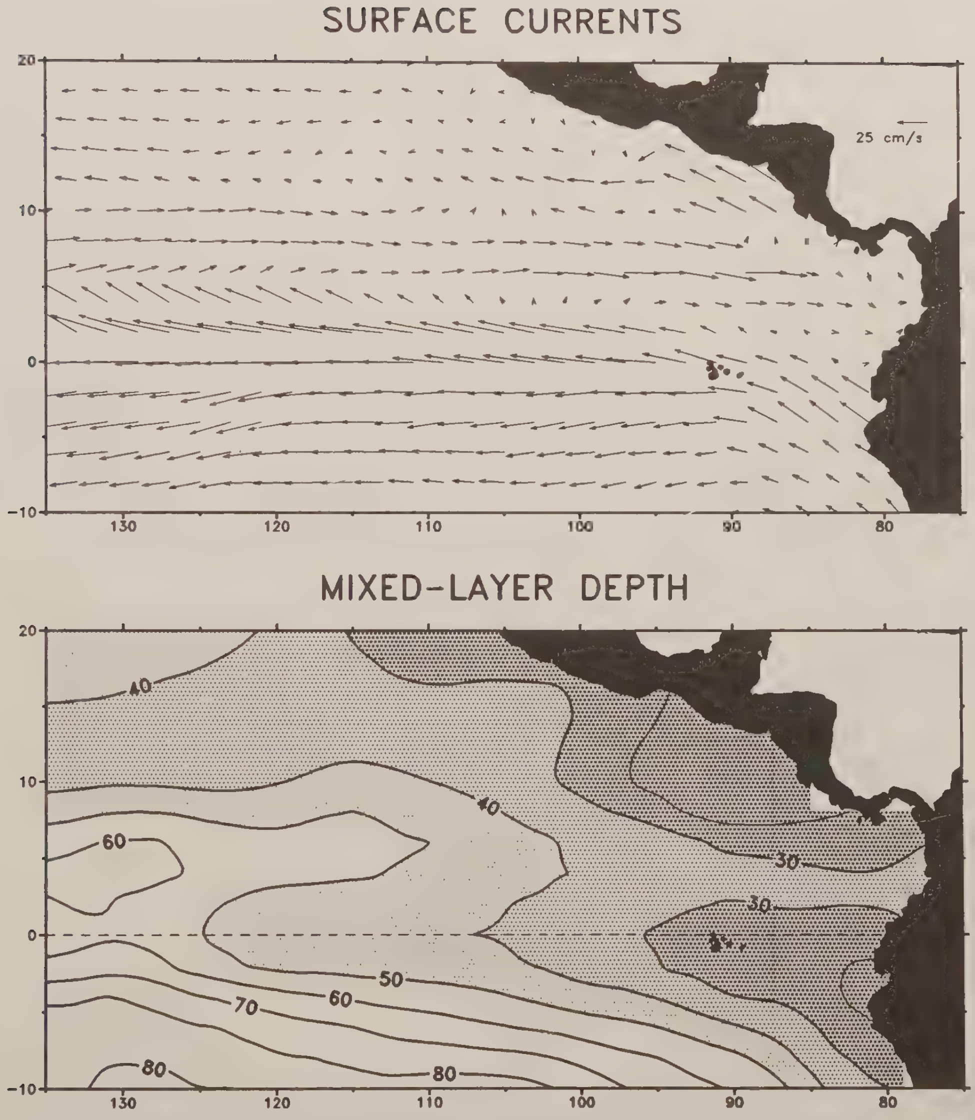

SURFACE CURRENTS
25 cm/s
20
10
0
−10
130
120
110
100
90
80
MIXED-LAYER DEPTH
40
40
60
30
30
50
60
70
80
80
20
10
0
−10
130
120
110
100
90
80

Fig. 3. Climatological August–November surface currents from ship drift data and mixed-layer depth (m) from XBT and MBT profiles.

m deeper than mixed-layer depth, except in the southwestern corner of the study area where the mixed layer is very deep.

Horizontal nutrient fluxes between boxes in the surface layer were calculated as the product of surface-current velocity, mean euphotic zone concentration, and mixed-layer depth times the length of the box edge (area of box side). A vertical flux into the surface layer (upwelling) was calculated as the product of net surface transport (out of a box) and nutrient concentration at the base of the euphotic zone. A vertical flux out of the surface layer (downwelling) was calculated as the product of net surface transport (into a box) and nutrient concentration in

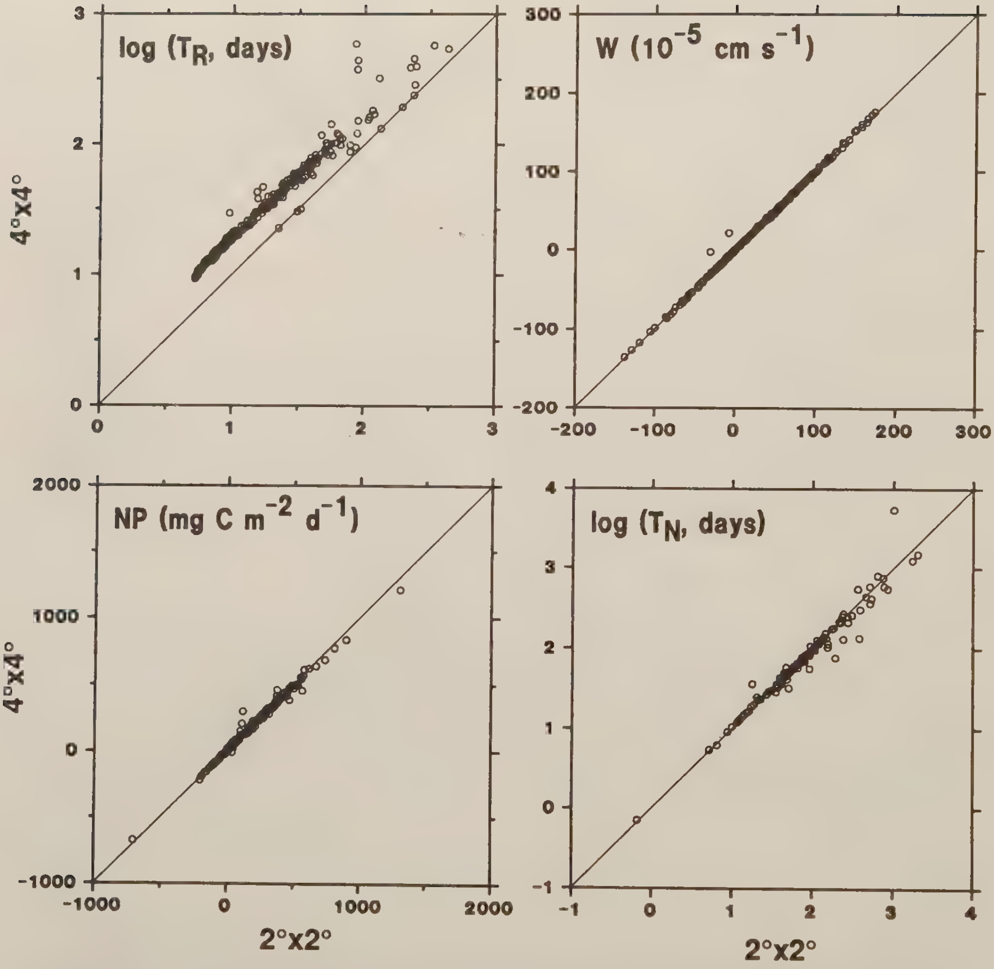
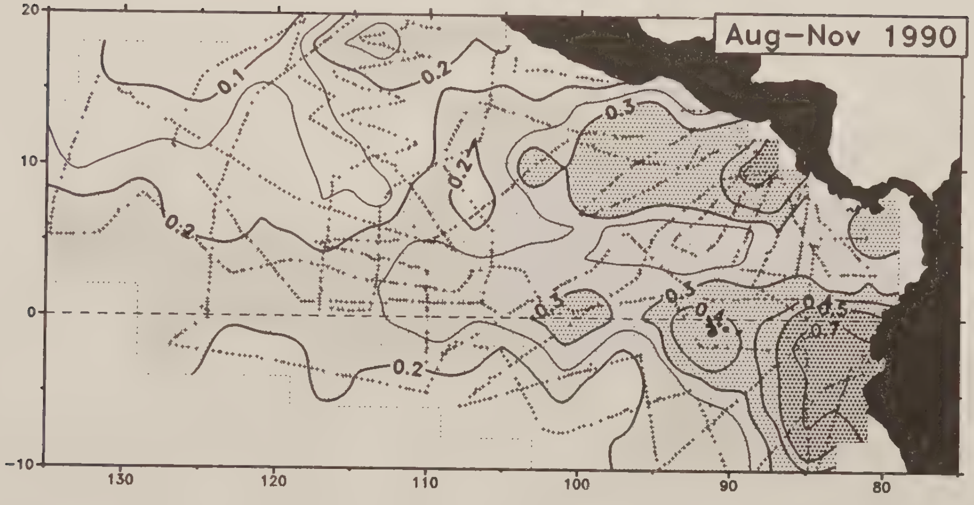


Fig. 4. Residence time (T_R), upwelling (W), new production (NP), and excess NO_3 persistence time (T_N) calculated at 2° × 2° and 4° × 4° resolution at model grid points.

the euphotic zone. Net NO_3 fluxes into the euphotic zone were converted to C production by the factor of 79.5 mg C (mmol N)$^{-1}$ [=106/16 mmol C (mmol N)$^{-1}$ × 12 mg C (mmol C)$^{-1}$]. This flux is equivalent to new production (NP, mg C m^{-2} d^{-1}).

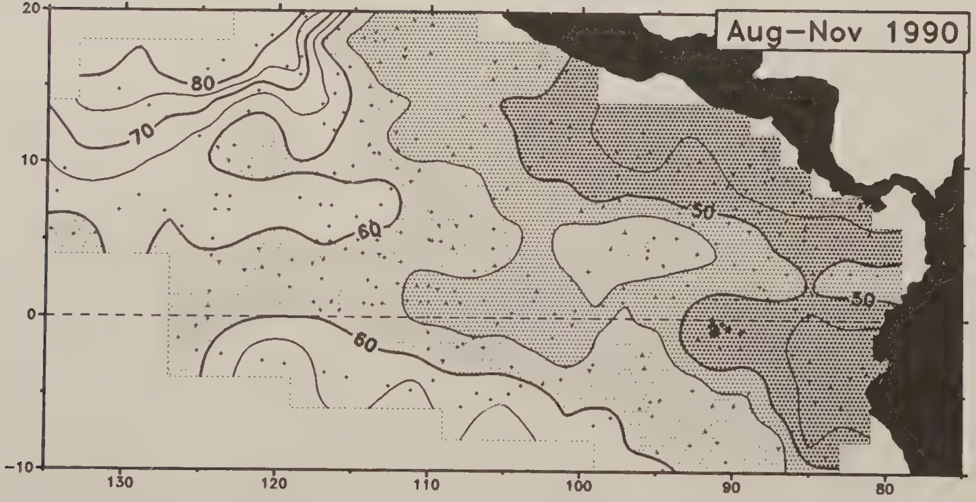
An index of the persistence of excess NO_3 in the euphotic zone was calculated as the excess NO_3 content of the euphotic zone [$Z_e(N_e - 4.0)$, mmol N m^{-2}] divided by net NO_3 input (mmol N m^{-2} d^{-1}). Excess NO_3 persistence time (T_N, d) represents the time required for phytoplankton uptake to deplete the excess NO_3 if NO_3 flux into the euphotic zone ceases. T_N is comparable to turnover times calculated from measured nutrient uptake rates and concentrations in the mixed layer or euphotic zone, although turnover times refer to uptake of the total, not excess, nutrient content.

Residence time of water within a box was calculated as the box volume divided by the total rate of inflow (or outflow). The effect of residence time of water in a box on rates estimated by the model was tested by comparing model results at 2° × 2° and 4° × 4° resolution. Residence time, rates of upwelling and new production, and excess NO_3



SURFACE CHLOROPHYLL

Aug–Nov 1990
0.1
0.2
0.3
0.2
0.2
0.5
0.3
0.4
0.5
0.7
0.2
20
10
0
−10
130
120
110
100
90
80



EUPHOTIC ZONE DEPTH

Aug–Nov 1990
80
70
60
50
50
60
20
10
0
−10
130
120
110
100
90
80

Fig. 5. Surface Chl concentration (mg m^{-3}) and euphotic zone depth (m), August–November 1990.

persistence time were calculated for the same grid points at each resolution. The results show that, although residence time increases by a factor of ~2 when box size is doubled, the other rates do not change (Fig. 4). The few points that do not fall along the 1 : 1 line represent boxes at the edges of the model domain where 4° × 4° boxes do not resolve the boundary as well as 2° × 2° boxes. Thus, rates derived from the model are not directly affected by model resolution and its effect on residence time.

Results

Observations—In August–November 1990, surface Chl was high (>0.2 mg m^{-3}) along both the equatorial and countercurrent divergences (Fig. 5). Values were highest (>0.4 mg m^{-3}) off the coast of Ecuador, around the Galapagos Islands, and at the Costa Rica Dome. The euphotic zone deepened from <45 m off Ecuador and Central America to >80 m in oligotrophic subtropical waters in the NW corner of the study area. Mean euphotic zone Chl (not shown, but directly related to Z_e by definition) showed the same basic pattern as surface Chl, except that relatively high values extended out beyond 110°W along the countercurrent divergence. Z_e was strongly correlated with the depth of the Chl maximum (Fig. 6, $r = 0.77$). In general, the Chl_{max} occurred below the 1% light level where $Z_e > 60$ m, toward the oligotrophic subtropical surface water masses of the North and South Pacific.

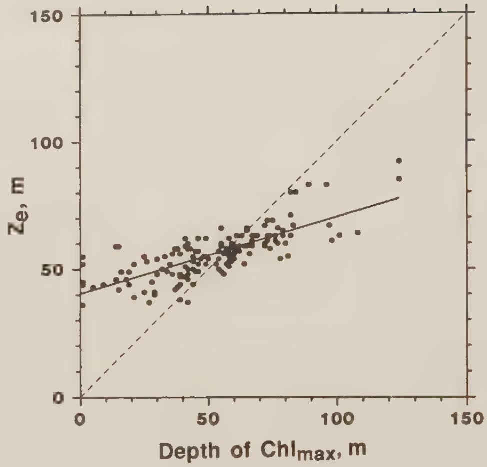


Fig. 6. Relationship between Z_e (m) and depth of the Chl_{max} (m), August–November 1990.

Phytoplankton productivity (*PP*) and productivity index ($PI = \int_z PP/\int_z \mathrm{Chl}$) were high [>600 mg C m^{-2} d^{-1} and >40 mg C (mg Chl)$^{-1}$ d^{-1}] along both the equatorial and countercurrent divergences out to 100°–110°W (Fig. 7). Along the countercurrent divergence, productivity was higher to the west of the Costa Rica Dome than in the dome itself (the surface Chl_{max} at 10°N, 88°W). A band of moderately high productivity extended west of 110°W along the equator.

NO_3 was depleted before SiO_4 or PO_4 in the 1986–1988 samples (Fig. 8, Table 1). The positive intercepts of the linear regressions of SiO_4 and PO_4 on NO_3 are 1.48 μM SiO_4 and 0.28 μM PO_4, both significantly different from zero ($P < 0.001$). The reciprocal of the slope of the PO_4-NO_3 regression is 16.1, compared to the N : P Redfield ratio of 16 : 1 (Redfield 1958). NO_3 decreases as water temperature increases (Fig. 9, Table 1). The regression line passes through 4 μM NO_3 at 25.4°C.

Nutrient-rich (>4 μM NO_3) surface waters were observed south of 2°N in 1986–1988 (Fig. 10). These correspond approximately to the equatorial and Peru Current surface-water masses described by Wyrtki (1967), although the nutrient-rich oceanic surface waters are not symmetric about the equator (*see also* Thomas 1979). The distribution of mean euphotic zone [NO_3] (N_e) indicates that nutrient-rich water is found deeper in the euphotic zone in tropical surface water north of the equatorial surface water and east of 105°W. [NO_3] at the bottom of the euphotic zone is as high or higher along the countercurrent divergence as along the equator.

Phytoplankton productivity observed in 1990 was significantly correlated with euphotic zone NO_3 (N_e, Fig. 11, $r = 0.47$). The significance of the Pearson correlation coefficient ($P < 0.0001$) was confirmed by a nonparametric test (Kendall's τ, Conover 1971). Normalizing productivity to Chl weakens the relationship slightly ($r = 0.42$), because N_e is related to euphotic zone pigment content through the derivation of Z_e.

Model—Divergence of surface currents results in strong upwelling along the equator, especially west of 115°W (Fig. 12). Weaker upwelling occurs along the countercurrent divergence at the coast and between 95° and 100°W, and in the northwest corner of the study area at the edge of the North Pacific subtropical gyre. The upwelling rates derived from ship drift data along the equatorial and countercurrent divergences are consistent with rates estimated by other methods (Fiedler 1992).

Estimated new production is positive in upwelling areas and in adjacent areas where unused NO_3 is advected horizontally from upwelling areas (Fig. 13). Highest rates occur in the equatorial divergence and in the

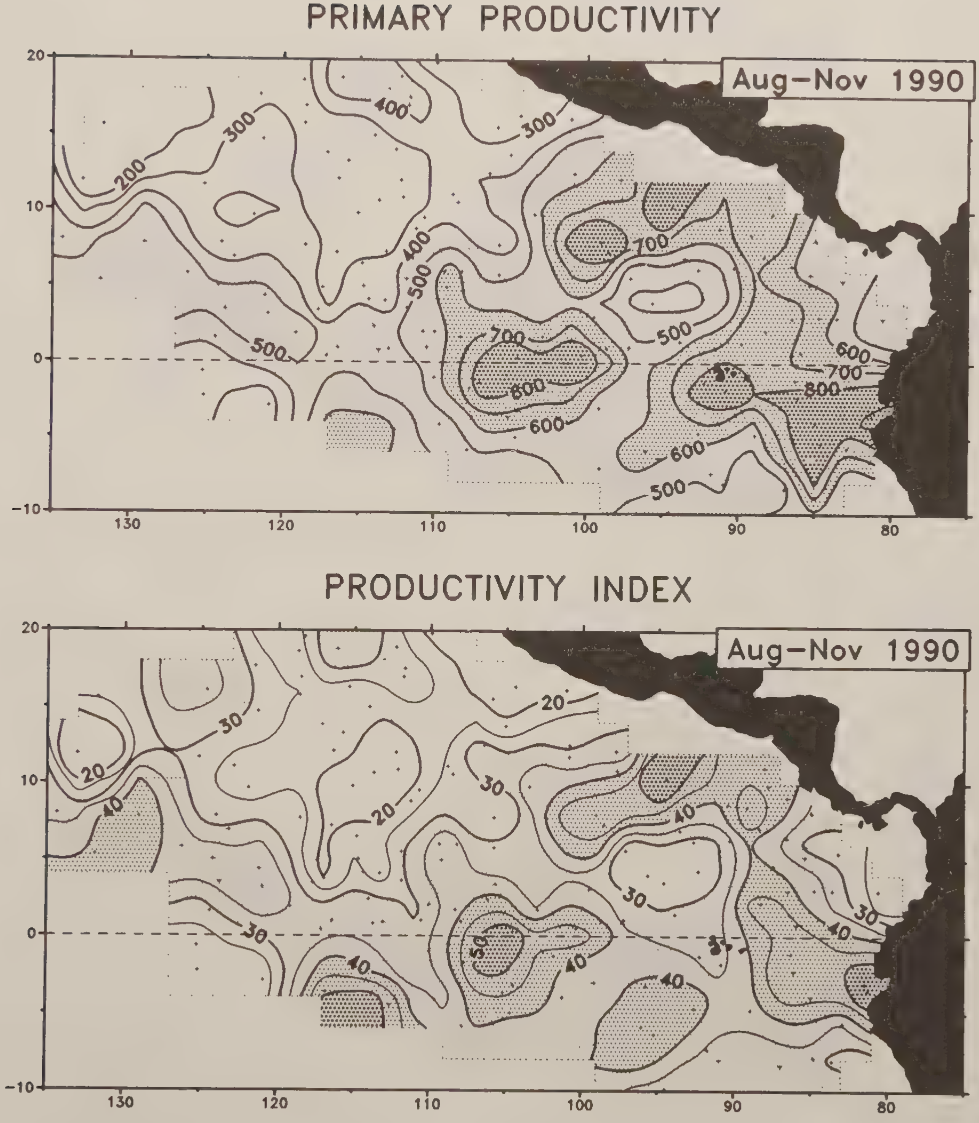

PRIMARY PRODUCTIVITY
Aug–Nov 1990
200
300
400
500
600
700
800
20
10
0
−10
130
120
110
100
90
80
PRODUCTIVITY INDEX
Aug–Nov 1990
20
30
40
50

Fig. 7. Phytoplankton productivity (mg C m^{-2} d^{-1}) and productivity index [mg C (mg Chl)$^{-1}$ d^{-1}], August–November 1990.

countercurrent divergence near the Costa Rica Dome. Estimated new production in upwelling areas ($W > 5 \times 10^{-5}$ cm s^{-1}) is significantly correlated with ^{14}C phytoplankton productivity measured in 1990 (Fig. 14, $r = 0.48$). The slope of the regression line is equivalent to an *f*-ratio (Eppley and Peterson 1979) and equals 0.29 (±0.11, 95% C.L.). Log-transformation does not significantly improve the regression relationship ($r = 0.50$).

Persistence of excess NO_3 in the euphotic zone, estimated from the model for 2° × 2° boxes with a positive net input of NO_3 (new production), is illustrated in Fig. 15. NO_3 persistence varies from 0.4 to >1,000 d

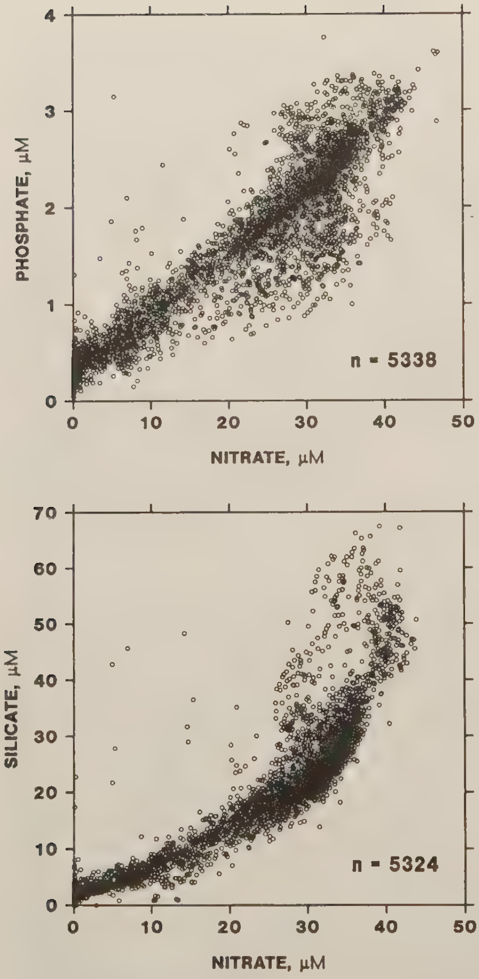


Fig. 8. PO_4-NO_3 and SiO_4-NO_3 relationships for the eastern tropical Pacific, August–November 1986–1988.

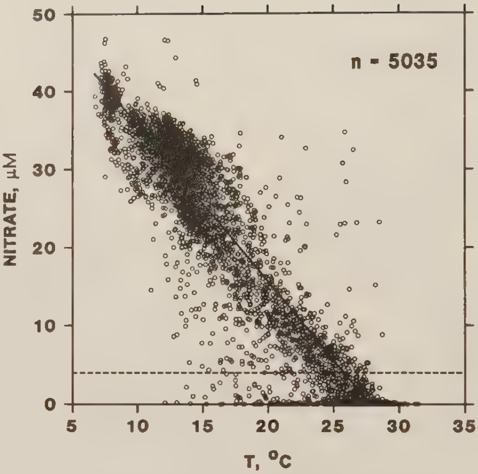


Fig. 9. NO_3-temperature relationship for the eastern tropical Pacific, August–November 1986–1988. Dashed line at 4 µM represents nominal concentration at which uptake by oceanic phytoplankton is saturated.

(median = 70). Persistence is shortest (<70 d) in the strong upwelling regions off Ecuador and along the northern edge of the equatorial divergence. Persistence is longest (>500 d) in tropical surface waters between the equatorial front and the coast of Central America, including waters at the Costa Rica Dome and along the countercurrent divergence.

Discussion

NO_3 can be depleted in the eastern tropical Pacific, but generally only in waters warmer than 25°C. Equatorial surface water rarely exceeds this temperature in August–November, except during El Niño. Tropical surface water is warmer than 27°C, even above the shallow thermocline in the countercurrent divergence at the eastern end of the countercurrent thermocline ridge (including the Costa Rica Dome). Euphotic zone waters are nutrient-rich (>4 µM N) along the equator and in tropical surface water north of 4°N and east of 105°W. We observed high phytoplankton biomass and productivity in these regions, especially in the two oceanic upwelling regions extending

Table 1. Nutrient and temperature relationships in the eastern tropical Pacific, August–November 1986–1988. All regressions are significant at $P < 0.001$.

$[SiO_4] = 0.635[NO_3] + 1.48$	$r = 0.89$	$n = 2{,}709$*
$[PO_4] = 0.062[NO_3] + 0.284$	$r = 0.94$	$n = 5{,}338$
$[NO_3] = -2.040T + 55.78$	$r = 0.95$	$n = 5{,}035$

* For $[NO_3] < 25$ µM.

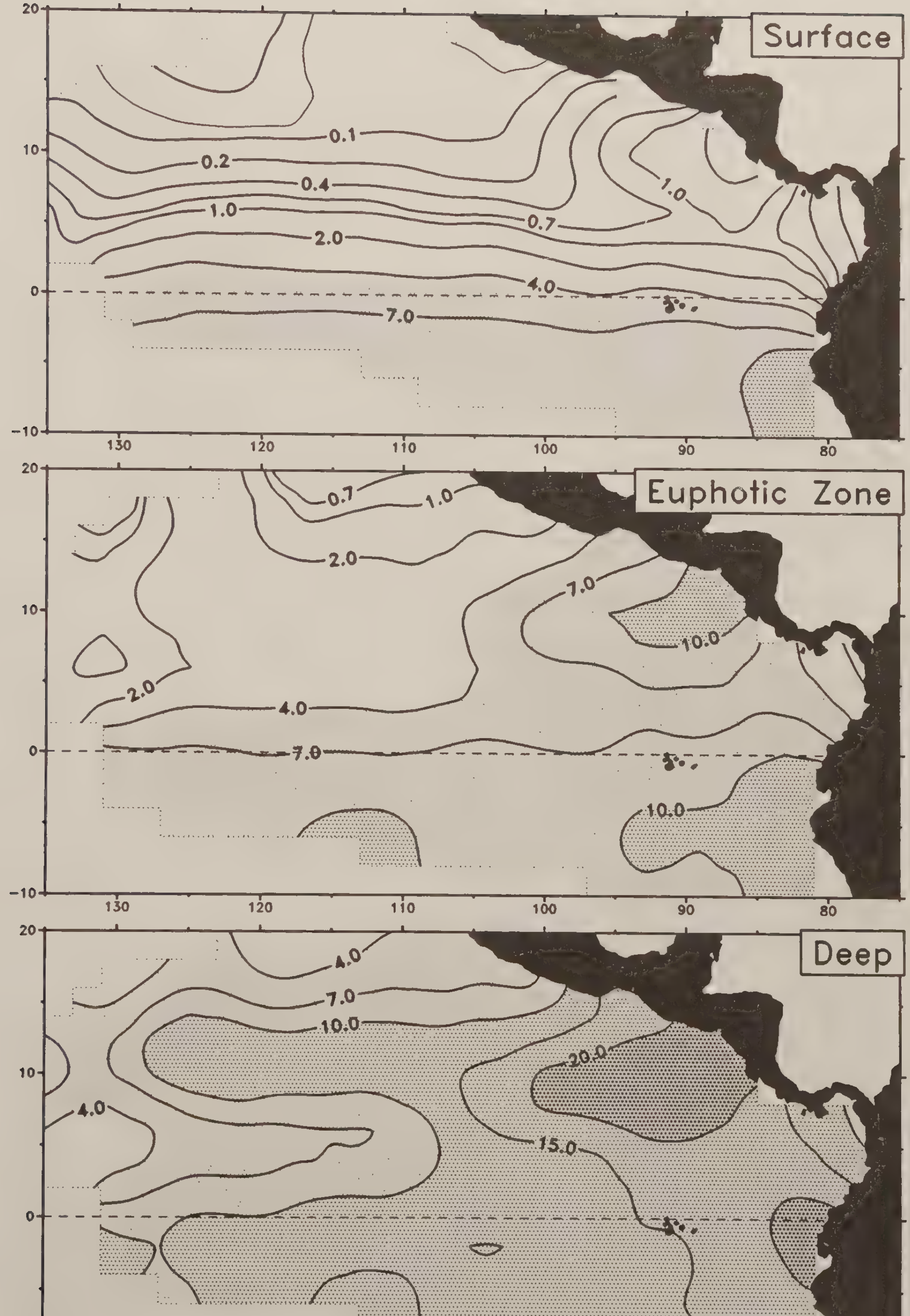

Surface
0.1
0.2
0.4
1.0
2.0
0.7
1.0
4.0
7.0
Euphotic Zone
0.7
1.0
2.0
7.0
10.0
2.0
4.0
7.0
10.0
Deep
4.0
7.0
10.0
20.0
4.0
15.0
20
10
0
-10
130
120
110
100
90
80

Fig. 10. [NO_3] (μM) at the surface, averaged over the euphotic zone, and at the euphotic zone depth, August–November 1986–1988.

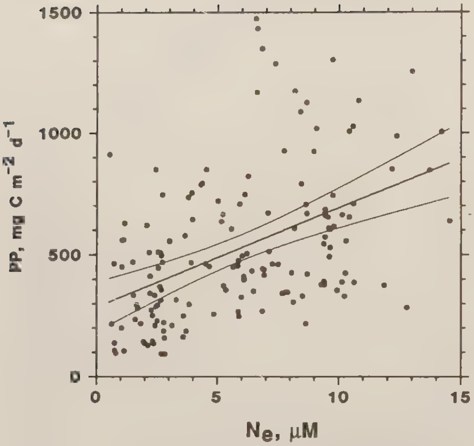


Fig. 11. Relationship between phytoplankton productivity (*PP*, mg C m^{-2} d^{-1}), August–November 1990, and 1986–1988 euphotic zone NO_3 (N_e, μM).

zonally to 105°W from the coast of Ecuador and the Costa Rica Dome.

Our measured rates of ^{14}C phytoplankton productivity are within the range reported by others using techniques to reduce trace metal contamination. We observed rates of 400–800 mg C m^{-2} d^{-1} in equatorial water between the Galapagos and 140°W. Rates observed previously in this region range between 400 and 1,000 (Chavez and Barber 1987; Chavez 1989; Chavez et al. 1990). Berger (1989), in a comprehensive global compilation of ^{14}C phytoplankton productivity rates (including measurements that may be biased by trace metal contamination), showed a range of 300–500 (up to 1,500 in a few small areas) in the eastern equatorial Pacific and in tropical waters east of 105°W. We observed rates of 200–400 mg C m^{-2} d^{-1} in tropical surface water west of 105°W. These values are comparable to other reported rates in this region: 200–500 at four stations along 110°W between 3° and 9°N (Chavez et al. 1990) and 100–200 along 126°W and 138°W (El-Sayed and Taguchi 1979). Berger (1989) showed a range of 100–300 in this region. EASTROPAC is the only other survey to have measured phytoplankton productivity in the eastern tropical Pacific over an area nearly as large as we did (Owen and Zeitzschel 1970). However, the EASTROPAC rates are much lower than more recent estimates, due to unresolved methodological problems (Banse and Yong 1990).

We observed productivity indices of 30–50 mg C (mg Chl)$^{-1}$ d^{-1} in equatorial and countercurrent divergence upwelling regions. Barber and Chavez (1991) reported areal means of 30.4–46.6 in the eastern equatorial Pacific between 84° and 140°W; Voiturez and Herbland (1977) reported "typical tropical" Atlantic values of 22–58. Mean productivity indices reported for coastal upwelling regions are in the same

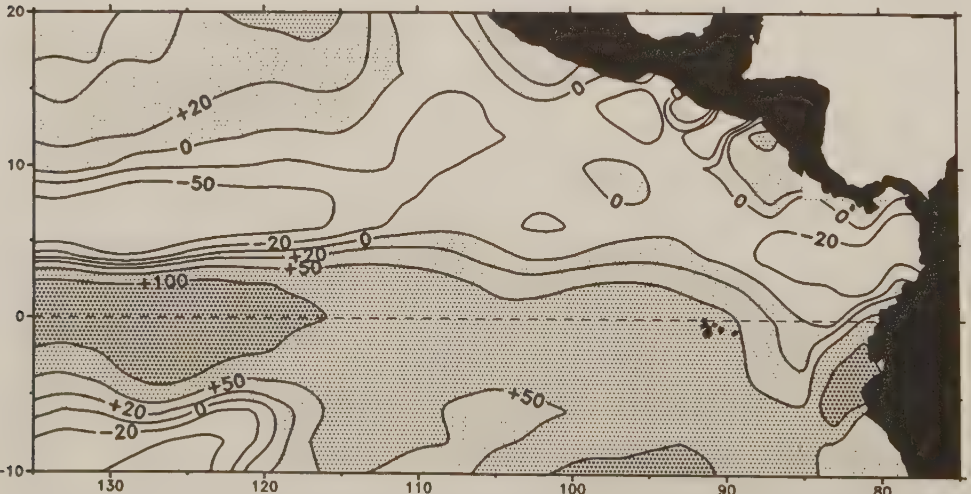
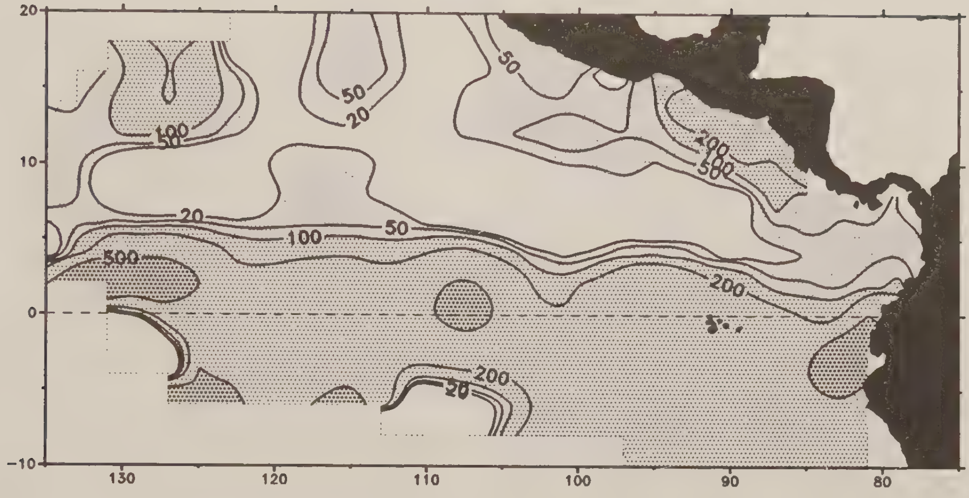


Fig. 12. August–November climatology of upwelling velocity (10^{-5} cm s^{-1}) at the base of the mixed layer derived from surface current divergence.



NEW PRODUCTION

20
10
0
−10
130
120
110
100
90
80
50
20
100
50
200
500
20
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50
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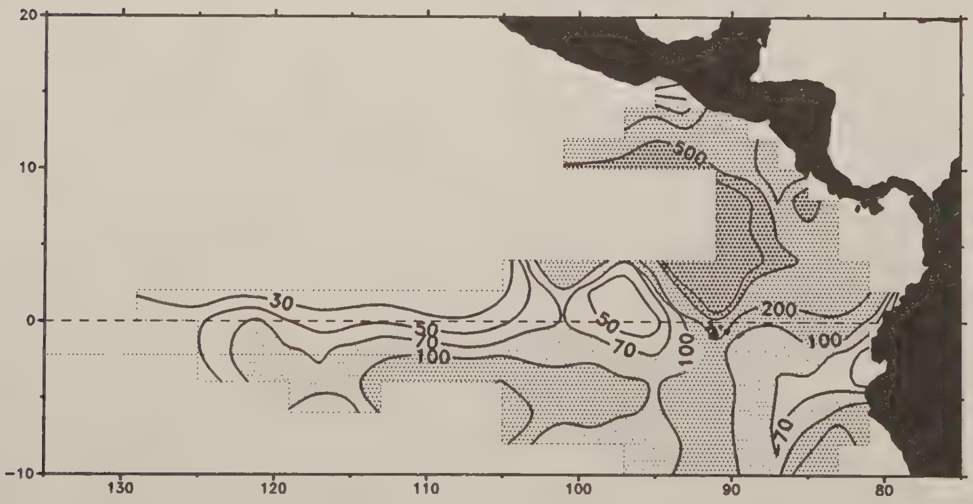
200
200
20



EXCESS NITRATE PERSISTENCE TIME

20
10
0
−10
130
120
110
100
90
80
500
30
50
70
100
50
70
100
200
100
70

Fig. 13. New production (mg C m^{-2} d^{-1}) and persistence of excess NO_3 (>4 μM) in the euphotic zone (d), estimated from the box model of NO_3 advective flux and uptake in the eastern tropical Pacific.

range: Peru—39 and 47 (Chavez and Barber 1987; Barber and Smith 1981); Northwest Africa—34 (Barber and Smith 1981); California Current—33 (Hayward and Venrick 1982). Lower productivity indices have been reported for other regions: 2–27 in the nutrient-limited North Pacific subtropical gyre and Sargasso Sea (Sharp et al. 1980; Prézelin and Glover 1991); 2–10 in the light-limited Southern Ocean (El-Sayed and Turner 1977; Holm-Hansen et al. 1977); 18.5 in the Southern California Bight (Eppley et al. 1985); and 8–22 in the subarctic Pacific (McAllister et al. 1960).

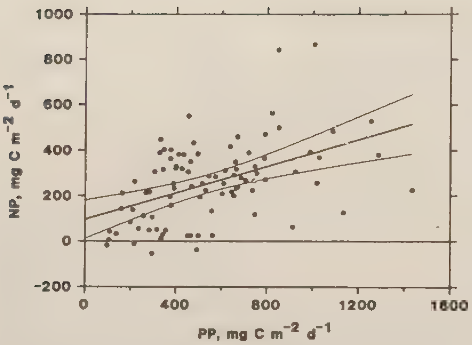


Fig. 14. Estimated new production (*NP*, mg C m^{-2} d^{-1}) vs. measured ^{14}C phytoplankton productivity (*PP*, mg C m^{-2} d^{-1}) at stations in climatological upwelling regions ($W > 5 \times 10^{-5}$ cm s^{-1}) of the eastern tropical Pacific, August–November 1990 ($n = 92$). Linear regression ±95% C.L.: $NP = 0.293PP + 95.4$, $r = 0.48$, $P < 0.00001$.

The apparent equatorial minimum at the Galapagos in the map of productivity index (Fig. 7) is defined by two stations ~100 km south of the islands. Barber and Chavez (1991), however, observed a relatively high mean productivity index at 19 stations in the Galapagos region, mostly along 92°W (50 km west of the islands) between 5°N and 5°S. Although the phytoplankton community in the equatorial Pacific is generally dominated by several small, solitary phytoplankton groups, relatively high diatom abundances have been observed near the Galapagos (Jimenez 1981). Differences in species composition between these two sites, especially in the relative abundance of diatoms, could affect the C : Chl ratio (Geider 1987), resulting in differences in productivity per unit Chl.

Although we do not have nutrient measurements available for our 1990 productivity stations, integrated phytoplankton productivity in the euphotic zone was significantly correlated with the NO_3 field observed in 1986–1988. This relationship suggests nutrient limitation of productivity in the nutrient-poor tropical and subtropical surface waters west of 105°W and north of 5°N in the eastern tropical Pacific. The strength of the relationship between productivity and $[NO_3]$ does not increase when productivity is normalized to Chl.

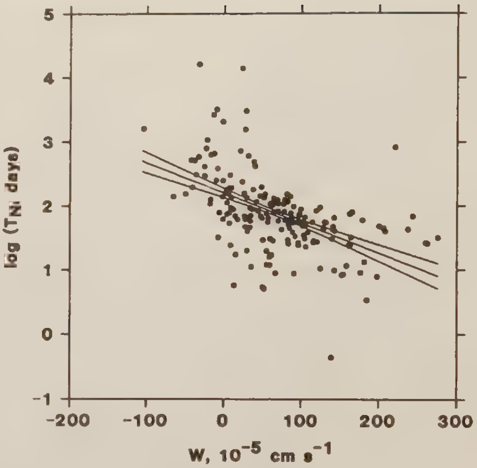


Fig. 15. Relationship between excess NO_3 persistence time (T_N, d) and upwelling rate (W, 10^{-5} cm s^{-1}) in the box model of NO_3 advective flux and uptake in the eastern tropical Pacific. Solid lines represent linear regression ±95% C.L.

Empirical and theoretical relationships between phytoplankton productivity per unit sea surface normalized to Chl (productivity index) and solar insolation have been explored by Platt et al. (1988) and Cullen (1990). General growth models reviewed by Cullen (1990) predict a *PI* of ~40 mg C (mg $Chl)^{-1}$ d^{-1} for a typical summer insolation in the eastern equatorial Pacific (70 Einst m^{-2} d^{-1}). *PI* is independent of nutrient limitation in such models and cannot be used to infer effects of nutrients on specific growth rates.

Our model indicates high rates of new production in the upwelling regions along the equator and at the Costa Rica Dome. New production also occurs in some downwelling areas, such as between the equatorial and countercurrent divergences east of 90°W and along the coast of Mexico to the northwest of the Costa Rica Dome. This production is driven by horizontal advection of unused NO_3 from adjacent upwelling areas.

Estimated new production based on climatological surface currents and 1986–1988 NO_3 distribution is significantly correlated with measured 1990 phytoplankton productivity. The relationship would presumably be stronger if we were able to use 1990 surface current and nutrient data to estimate new production. The slope of the regression line is 0.29 (±0.11), representing an average *f*-ratio (new/total production). Eppley and Peterson (1979) estimated *f*-ratios of 0.13–0.30 for the water types found in the eastern tropical Pacific (transitional, equatorial divergence, and inshore waters), and Dugdale (1976) reported measured *f*-ratios of 0.17–0.21. Eppley and Peterson (1979) found that the *f*-ratio increases with total productivity, but the scatter in our results is too great to resolve a nonlinear relationship.

The major discrepancy between the estimated and measured rates is the difference in zonal gradients of productivity. Measured rates of phytoplankton productivity decline to the west along both the countercurrent and equatorial divergences. In contrast, the model estimates relatively high rates of upwelling and new production along the equator west of the Galapagos and at the edge of the subtropical gyre. This difference may indicate that the model's direct relationship between transports and mixed-layer depth, which increases from east to west, is inadequate to describe the advective regime.

The extent of HNLC conditions in the eastern tropical Pacific is delimited by the region of excess NO_3 persistence in Fig. 13 (cf. Figs. 5 and 10). Excess NO_3 persistence time (T_N) is an index of limitation or control of NO_3 uptake (new production). T_N is inversely correlated with upwelling rate (W, Fig. 15, $r = -0.52$). This result is partially a consequence of the definition of T_N [$=Z_e(N_e - 4)/N'$, where N' = net NO_3 input], because W is weakly correlated with $Z_e(N_e - 4)$ ($r = +0.14$) and positively correlated with N' ($r = +0.37$).

Turnover times of euphotic zone N in the oligotrophic North Pacific central gyre are 3–15 d (Eppley et al. 1973). Turnover times in coastal upwelling systems are also on the order of a few days (Zimmerman et al. 1987). In contrast, NO_3 uptake rates measured at the surface in the central equatorial Pacific (150°W) indicate a NO_3 turnover time of >120 d and a T_N of >35 d (Wilkerson and Dugdale 1992), which is consistent with the model estimates of excess NO_3 persistence along the equator. In weak upwelling and downwelling HNLC conditions in the eastern tropical Pacific, NO_3 persists for >100 d at concentrations that should saturate uptake by phytoplankton, which indicates limitation or control of uptake and new production by a factor other than NO_3. Alternative hypotheses include control of phytoplankton biomass by grazing and limitation of NO_3 uptake by Fe deficiency (Cullen 1991). Our observations and model results are not adequate for conclusive tests of these hypotheses.

Our survey of the eastern tropical Pacific confirmed moderately high rates of phytoplankton production in oceanic upwelling regions along the equatorial and countercurrent divergences. In nutrient-poor regions of the eastern tropical Pacific, productivity is apparently limited by NO_3 availability. A box model of NO_3 flux, based on observed surface currents and NO_3 distribution, indicates that rates of NO_3 utilization or new production in upwelling regions is much lower than the rate of input of upwelled NO_3 into the euphotic zone. Excess NO_3 persists in the euphotic zone and is advected to adjacent weak upwelling and downwelling regions, where it can persist for >200 d. Grazing, Fe deficiency, or other hypotheses of limitation of productivity must explain this long persistence of NO_3 in the well-lighted HNLC waters of the eastern tropical Pacific.

References

BANSE, K., AND M. YONG. 1990. Sources of variability in satellite-derived estimates of phytoplankton production in the eastern tropical Pacific. J. Geophys. Res. **95:** 7201–7215.

BARBER, R. T., AND F. P. CHAVEZ. 1991. Regulation of primary productivity rate in the equatorial Pacific. Limnol. Oceanogr. **36:** 1793–1802.

———, AND R. L. SMITH. 1981. Coastal upwelling ecosystems, p. 31–68. *In* A. R. Longhurst [ed.], Analysis of marine ecosystems. Academic.

BERGER, W. H. 1989. Appendix: Global maps of ocean productivity, p. 429–455. *In* W. H. Berger et al. [eds.], Productivity of the ocean: Present and past. Wiley.

CHAVEZ, F. P. 1989. Size distribution of phytoplankton in the central and eastern tropical Pacific. Global Biogeochem. Cycles **3:** 27–35.

———, AND R. T. BARBER. 1987. An estimate of new production in the equatorial Pacific. Deep-Sea Res. **34:** 1229–1243.

———, K. R. BUCK, AND R. T. BARBER. 1990. Phytoplankton taxa in relation to primary production in the equatorial Pacific. Deep-Sea Res. **37:** 1733–1752.

CONOVER, W. J. 1971. Practical nonparametric statistics. Wiley.

CULLEN, J. J. 1990. On models of growth and photosynthesis in phytoplankton. Deep-Sea Res. **37:** 667-683.

———. 1991. Hypotheses to explain high-nutrient conditions in the open sea. Limnol. Oceanogr. **36:** 1578–1599.

DUGDALE, R. C. 1976. Nutrient cycles, p. 141–172. *In* D. H. Cushing and J. J. Walsh [eds.], The ecology of the seas. Saunders.

EL-SAYED, S. Z., AND S. TAGUCHI. 1979. Phytoplankton standing crop and primary productivity in the tropical Pacific, p. 241–286. *In* J. L. Bischoff and D. Z. Piper [eds.], Marine geology and oceanography of the Pacific manganese nodule province. Plenum.

———, AND J. T. TURNER. 1977. Productivity of the Antarctic and subtropical regions: A comparative study, p. 463–504. *In* Polar oceans. Proc. SCOR/SCAR Conf.

EPPLEY, R. W., AND B. J. PETERSON. 1979. Particulate organic matter flux and planktonic new production in the deep ocean. Nature **282:** 677–680.

———, E. H. RENGER, E. L. VENRICK, AND M. M. MULLIN. 1973. A study of plankton dynamics and nutrient cycling in the central gyre of the north Pacific Ocean. Limnol. Oceanogr. **18:** 534–551.

———, E. STEWART, M. R. ABBOTT, AND U. HEYMAN. 1985. Estimating ocean production from satellite chlorophyll. Introduction to regional differences and statistics for the Southern California Bight. J. Plankton Res. **7:** 57–70.

FIEDLER, P. C. 1992. Seasonal climatologies and variability of eastern tropical Pacific surface waters. NOAA Tech. Rep. NMFS. In press.

———, F. P. CHAVEZ, D. W. BEHRINGER, AND S. B. REILLY. 1992. Physical and biological effects of Los Niños in the eastern tropical Pacific, 1986–1989. Deep-Sea Res. **39:** In press.

GEIDER, R. J. 1987. Light and temperature dependence of the carbon to chlorophyll *a* ratio in microalgae and cyanobacteria: Implications for physiology and growth of phytoplankton. New Phytol. **106:** 1–34.

HAYWARD, T. L., AND E. L. VENRICK. 1982. Relation between surface chlorophyll, integrated chlorophyll and primary production. Mar. Biol. **69:** 247–252.

HOLM-HANSEN, O., S. Z. EL-SAYED, G. A. FRANCESCHINI, AND R. L. CUHEL. 1977. Primary production and factors controlling phytoplankton growth in the Southern Ocean, p. 11–50. *In* G. A. Llano [ed.], Adaptations within the Antarctic ecosystems. Gulf.

JENKINS, W. J. 1988. Nitrate flux into the euphotic zone near Bermuda. Nature **331:** 521–523.

JIMENEZ, R. 1981. Composition and distribution of phytoplankton in the upwelling systems of the Galapagos Islands, p. 327–338. *In* F. A. Richards [ed.], Coastal upwelling. Coastal Estuarine Sci. V. 1. AGU.

LEVITUS, S. 1982. Climatological atlas of the world ocean. NOAA Prof. Pap. 13. U.S. GPO.

MCALLISTER, C. D., T. R. PARSONS, AND J. D. H. STRICKLAND. 1960. Primary productivity and fertility at Station "P" in the northeast Pacific Ocean. J. Cons. Cons. Int. Explor. Mer **25:** 240–259.

MACISAAC, J. J., AND R. C. DUGDALE. 1969. The kinetics of nitrate and ammonia uptake by natural populations of marine phytoplankton. Deep-Sea Res. **16:** 45–57.

MOREL, A. 1988. Optical modeling of the upper ocean in relation to its biogenous matter content (Case 1 waters). J. Geophys. Res. **93:** 10,749–10,768.

OWEN, R. W., AND B. ZEITZSCHEL. 1970. Phytoplankton production: Seasonal change in the oceanic eastern tropical North Pacific. Mar. Biol. **7:** 32–36.

PLATT, T., S. SATHYENDRANATH, C. M. CAVERHILL, AND M. R. LEWIS. 1988. Ocean primary production and available light: Further algorithms for remote sensing. Deep-Sea Res. **35:** 855–879.

PRÉZELIN, B. B., AND H. E. GLOVER. 1991. Variability in time/space estimates of phytoplankton, biomass and productivity in the Sargasso Sea. J. Plankton Res. **13**(suppl.): 45–67.

REDFIELD, A. C. 1958. The biological control of chemical factors in the environment. Am. Sci. **46:** 205–221.

RILEY, G. A. 1956. Oceanography of Long Island Sound, 1952–1954. 4. Production and utilization of organic matter. Bull. Bingham Oceanogr. Collect. **15:** 324–344.

ROEMMICH, D. 1989. Mean transport of mass, heat, salt and nutrients in southern California coastal waters: Implications for primary production and nutrient cycling. Deep-Sea Res. **36:** 1359–1378.

SAPOZHNIKOV, V. V., AND L. I. GALERKIN. 1973. Calculation of primary production in tropical waters from the upward influx of biogenic elements, p. 67–72. *In* M. E. Vinogradov [ed.], Life activity of pelagic communities in the ocean tropics. Israel Program Sci. Transl.

SARMIENTO, J. L., G. THIELE, R. M. KEY, AND W. S. MOORE. 1990. Oxygen and nitrate new production and remineralization in the North Atlantic subtropical gyre. J. Geophys. Res. **95:** 18,303–18,315.

SHARP, J. H., M. J. PERRY, E. H. RENGER, AND R. W. EPPLEY. 1980. Phytoplankton rate processes in the oligotrophic waters of the central North Pacific Ocean. J. Plankton Res. **2:** 335–353.

SVERDRUP, H. U., M. W. JOHNSON, AND R. H. FLEMING. 1942. The oceans. Prentice-Hall.

THOMAS, W. H. 1979. Anomalous nutrient chlorophyll interrelationships in the offshore eastern tropical Pacific Ocean. J. Mar. Res. **37:** 327–335.

VOITUREZ, B., AND A. HERBLAND. 1977. Étude de la production pélagique de la zone équatoriale de l'Atlantique à 4°W. Cah. ORSTOM Ser. Oceanogr. **25**: 313–331.

WILKERSON, F. P., AND R. C. DUGDALE. 1992. Measurements of nitrogen productivity in the equatorial Pacific. J. Geophys. Res. **97**: 669–679.

WYRTKI, K. 1964. The thermal structure of the eastern Pacific Ocean. Dtsch. Hydrogr. Z. Suppl., p. 1–84.

———. 1967. Circulation and water masses in the eastern equatorial Pacific Ocean. Int. J. Oceanol. Limnol. **1**: 117–147.

YENTSCH, C. S. 1990. Estimates of "new production" in the mid-North Atlantic. J. Plankton Res. **12**: 717–734.

ZIMMERMAN, R. C., J. N. KREMER, AND R. C. DUGDALE. 1987. Acceleration of nutrient uptake by phytoplankton in a coastal upwelling ecosystem: A modeling analysis. Limnol. Oceanogr. **32**: 359–367.

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Detecting Trends in Harbor Porpoise Abundance from Aerial Surveys Using Analysis of Covariance

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Abstract.–Aerial surveys designed to detect trends in the abundance of harbor porpoise *Phocoena phocoena* were conducted each autumn, 1986 through 1990. The number of porpoise seen per kilometer of survey effort was used as an index of abundance. Based on these surveys, an analysis of covariance was used to model porpoise abundance. Year was treated as a covariate, and factors which affected sighting rates were included as categorical variables. No significant changes were seen in the abundance of porpoise over the five survey years. Monte Carlo simulations were performed to determine the power of the ANCOVA to detect trends in abundance. We conclude that the ability to detect trends is poor if traditional levels of statistical significance ($\alpha = 0.05$) are used. A larger α-error may be appropriate in the management context of this species and increases the power to detect trends. Additional survey years similarly improve the power to detect trends. Based on the results of the simulations, we suggest that power should be defined to include only the detection of the correct trend when two-tailed tests are employed.

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Harbor porpoise *Phocoena phocoena* are caught incidentally during halibut fishing with gillnets along the central California coast (Diamond and Hanan 1986; Hanan et al. 1986, 1987; Barlow 1987; Barlow and Hanan 1990). To assess the potential impact of this fishery mortality, ship and aerial surveys have been used to estimate the abundance of harbor porpoise along the coast of California, Oregon, and Washington (Barlow 1988, Barlow et al. 1988). These authors showed that although aircraft can be used to survey a large area very quickly, abundance estimates from aerial surveys must be multiplied by a very large and uncertain correction factor to account for the majority of animals that will be underwater at any given instant. For this reason, ship surveys were concluded to be preferable for estimating absolute porpoise abundance.

The requirements are, however, less stringent if the only goal is to detect trends in the abundance of porpoise over time, rather than determining absolute abundance. The ability of aircraft to cover great distances relatively quickly and inexpensively makes them a logical platform for such surveys. If the fraction of animals detected from the air does not change over time, the correction factor becomes irrelevant, and indices of relative abundance can be used in place of absolute abundance measures.

We describe a series of five aerial surveys for harbor porpoise conducted in central California during autumn of 1986, 1987, 1988, 1989, and 1990. These surveys were designed specifically to detect changes in porpoise abundance. We used twin-engine aircraft to fly predetermined transect lines which zigzagged up the coast between Point Conception and the mouth of the Russian River (Fig. 1). Line transect methods were used with one observer on each side of the aircraft and a belly-port observer. A fourth person recorded information pertaining to sightings of porpoises and sighting conditions. Each year within the survey period, the transect lines were repeated 3–7 times, depending on weather conditions.

The number of porpoise seen per kilometer of search effort was used as a measure of relative abundance. A stepwise analysis of covariance procedure (ANCOVA) with year as the covariate was used to identify the best model describing porpoise seen per kilometer. Standard ANCOVA F-ratio tests were applied to determine whether a significant trend with year is present. Monte Carlo methods were used to determine the power of this test to detect known trends in abundance.

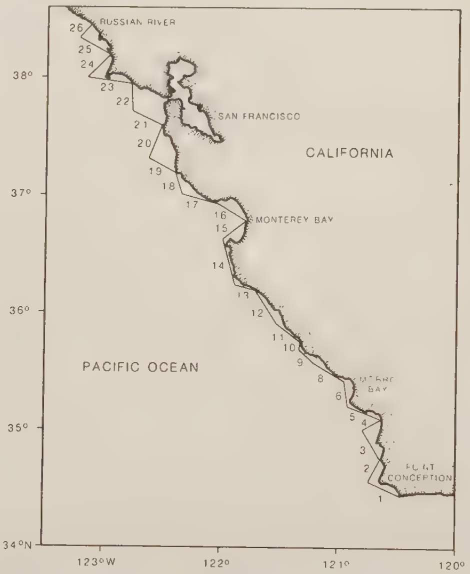

Figure 1

Flight transects for aerial survey of harbor porpoise in central California, 1986–90. Transect 7 was combined with transect 8 after 1986 and is not shown.

Methods

Field methods

The surveys were established to monitor changes in abundance within the range of porpoise/gillnet fishery interactions (Point Conception to Russian River, California). Surveys were started only when there was a good likelihood of completing at least half of the survey (Point Conception to Monterey, or Monterey to Russian River) under good weather conditions. They were halted when viewing conditions deteriorated below acceptable levels (sea state higher than Beaufort 4 or 5, excessive dark cloud cover, rain, or fog).

A series of predetermined locations marking the beginning and end of each transect was entered into the aircraft's LORAN C navigational receiver to give the pilot a course to follow. The transects zigzagged in a generally northward progression between shore and roughly the 50-fathom (91-m) contour (Fig. 1). Sightings at the endpoint of a transect were very rare, and duplication at the start of the next transect did not occur. The transect lengths ranged from 5.2 to 44.8 km and averaged 24.8 km. The aircraft maintained an altitude of approximately 213 m and speeds of 90–100 knots (167–185 km/hour). To reduce sun glare, surveys were conducted only from south to north.

The surveys were flown in a twin-engine, high-wing, seven-passenger aircraft with the rear seat removed (Partenavia P68). Two observers sat behind the pilot and copilot seats and looked out the side windows; a third observer (belly observer) lay on the floor on his/her stomach just behind the right-side observer's seat and surveyed the water below the airplane through a 25 × 30-cm rectangular viewing port. Starting in 1988, the side windows were fitted with plexiglas bubble-type windows, allowing the side observers to see from the horizon to directly under the plane. This created an overlap with the belly observer's field of view; however, this did not result in double counting because the observers were in constant communication and discussed all possible sighting duplicates as they occurred.

The data recorder sat in the copilot position and recorded flight information, including location (latitude and longitude), time, weather (% cloud cover, Beaufort sea state, and sun position), viewing conditions, and porpoise sighting information. The data recorder entered weather and viewing conditions at the start of each transect and whenever conditions changed. Each observer subjectively evaluated viewing conditions as excellent, good, poor or "off effort," depending on estimated viewing depth into the water, sun glare, and sea state. To simplify the recording procedure and enhance accuracy of the data, a lap-top computer connected to the LORAN C navigational receiver replaced the hand-written flight log during the 1988–90 surveys.

The pilot, recorder, and observers communicated through headsets and voice-activated microphones. All communication was recorded on a central tape recorder. Additionally, each observer used a hand-held tape recorder for storage of individual sighting information. The two side observers used hand-held inclinometers to measure declination angles in degrees to the animals sighted. Due to space limitations, the belly observer could not use an inclinometer and estimated angles using marks applied to the viewing port. The observers changed positions approximately every 1–1.5 hours and between flights.

The observers actively searched (were "on effort") from start to finish of a transect, except when circling or when they declared themselves "off effort" because

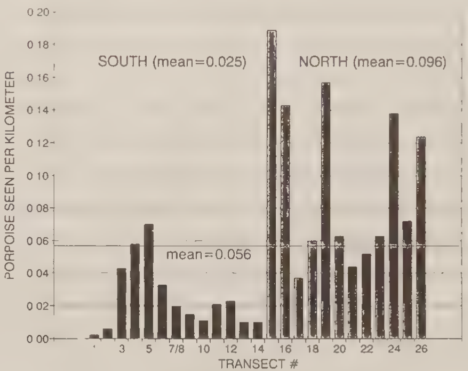

Figure 2

Porpoise seen per kilometer in transects 1 through 26 for 1986–90 surveys (including Beaufort sea states 0–3 and clear skies only). For the analysis, transects were divided into two areas at Point Pinos (between transects 14 and 15): south (low abundance) and north (high abundance).

of poor sighting conditions. The pilot circled on porpoise sightings if there was any question about species identification or number of porpoise. Additional sightings made while circling were recorded as "off effort" sightings and were not included in the analyses.

During the first survey year (1986), observers reported all marine mammals sighted. However, the large number of California sea lion sightings took a disproportionate amount of time, so only harbor porpoise were recorded in 1987–90. Following the surveys, the data in the flight log or computer were checked for accuracy and, if needed, compared with the tape recordings. The data were transferred into microcomputer databases for summary and analysis.

Analytical methods

Individual flight segments during which all sighting conditions were constant were combined to measure porpoise per kilometer in relation to each of the sighting variables. These variables included Beaufort sea state, cloud cover, viewing condition, individual observers, and an *a posteriori* geographic subdivision chosen on the basis of apparent porpoise abundance: south (low abundance) and north (high abundance) (Fig. 2). This subdivision was created to correct for slight interannual differences in survey effort for high- and low-density areas, caused by bad weather.

Cloud cover was recorded as a percentage and later coded into the categories "clear" (0–24%) and "cloudy" (25–100%). Sighting efficiency and sample sizes decreased dramatically when Beaufort sea state was higher than 3, so only segments with Beaufort 0–3 were used. Beaufort 0 was combined with Beaufort 1 because there was very little survey effort at Beaufort 0.

The data were fitted to an analysis of covariance (ANCOVA) model of the form:

$$P = \mu + \alpha_1 + \alpha_2 + \ldots + \delta(y - \bar{y}) + \varepsilon \qquad (1)$$

where P represents the log-transformed ($\log_e$) value of porpoise per kilometer, μ is the mean value of P, the α represent qualitative factors influencing observed porpoise abundance, δ represents the coefficient for the covariate year (y), $\bar{y}$ is the mean value of y, and ε is a random error term. Such an additive model for logarithmic values is equivalent to a model describing multiplicative effects on the untransformed number of porpoise seen. This was deemed appropriate because sighting conditions affect the fraction of porpoise seen but not the absolute density of porpoise present. Because of the logarithmic transformation, a linear increase or decrease in the covariate would be interpreted as an exponential increase or decrease in porpoise abundance. The constant 0.001 was added to each value before transformation to avoid trying to take the logarithm of zero. This logarithmic transformation also made the data more nearly normal (Fig. 3).

It was not possible to include all potential variables in the model selection procedure, because this would have caused overstratification of the data. Individual observer effects were excluded because not all observers collected data each year, resulting in a large number of missing cell values. Viewing condition was also excluded because it is somewhat redundant with sea state and cloud cover and it is more subjective. Previous nonparametric tests of individual observer effects and viewing conditions with three years of data (Forney et al. 1989) yielded no significant differences in observed numbers of porpoise per kilometer.

In the ANCOVA, the data were weighted by the number of kilometers flown to correct for variability due to unequal sample sizes. A stepwise selection procedure with the SAS procedure GLM (Joyner 1985) was used to determine the best model for the observed data. At each step, all appropriate parameters and interaction effects were tested individually. The most significant parameter was added to the model, based on a criterion level of $\alpha = 0.05$. Each included variable was retested for significance at each subsequent step of the procedure.

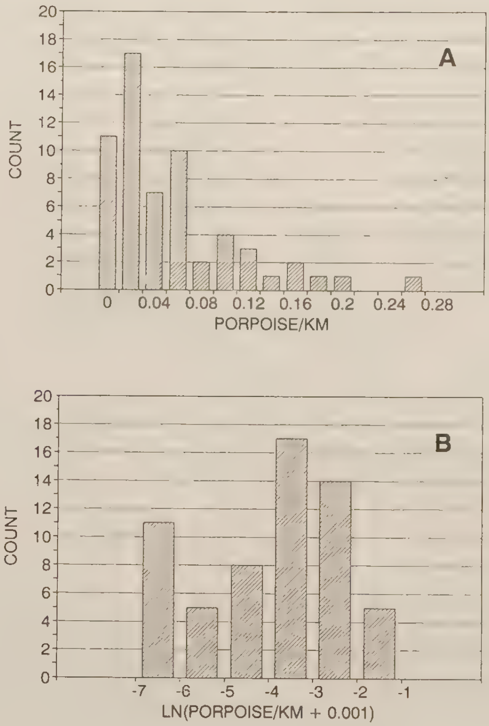

Figure 3
Distribution of observed porpoise/km values (A), and log-transformed porpoise/km values (B) for five years of aerial survey data. The transformation was ln(x + 0.001), where x is the observed number of porpoise/km.

Table 1
Average number of harbor porpoise seen per kilometer of search effort for 1986–90 aerial surveys. Numbers of porpoise seen per number of kilometers surveyed are given in parentheses. Categories are defined in the text. Overall mean number of porpoise per kilometer is 0.047 (796/16948).

Area	Cloud cover	Beaufort 0, 1	2	3
South	Clear	0.036 (75/2075)	0.024 (54/2248)	0.013 (24/1918)
	Cloudy	0.030 (31/1026)	0.015 (15/974)	0.006 (3/518)
North	Clear	0.163 (170/1042)	0.106 (229/2165)	0.046 (84/1814)
	Cloudy	0.058 (30/521)	0.039 (59/1530)	0.020 (22/1117)

Simulation methods

Once the best model had been selected (see Results), Monte Carlo simulations were performed to determine the power of the ANCOVA to correctly detect a given trend in porpoise abundance. The analysis of power was divided into two main steps: (1) Simulations without a trend, to determine whether the procedure can create and correctly analyze simulated data; and (2) simulations with trends, to estimate how often the procedure correctly identifies a known trend in harbor porpoise abundance. Annual changes of ±5% and ±10% were tested over periods of five, six, eight, and ten years.

The random data sets were generated using the parameters and error structure obtained for the actual data from the best model (see Results). First, the expected logarithmic value of porpoise per kilometer for each combination of conditions was calculated from the fitted parameters. A random error term for each expected value was then drawn from a normal distribution with a mean of zero and standard error from the ANCOVA results of the best model. To allow weighted analysis of the simulated data, this error term was weighted inversely, i.e., multiplied times $\sqrt{(1/w)}$, where w is the number of kilometers flown under the given conditions. A set of 60 values for w, one for each of the 60 simulated porpoise-per-kilometer values, was obtained for each year by randomly selecting the actual numbers of kilometers flown from one of the five survey years. Complete yearly sets were chosen rather than individual values to avoid unlikely combinations of kilometers flown.

A yearly trend was incorporated into the simulation data by multiplying the calculated value of porpoise per kilometer times a factor representing the desired exponential change in porpoise abundance. To make the simulated data more like potential real data, all values were rounded to yield only integer values of porpoise over the given number of kilometers flown. In addition, to prevent unfeasible values of porpoise per kilometer, a new error term was drawn if the original one resulted in a value which was negative or greater than 0.4 porpoise per kilometer. The highest value observed in 1986–90 was 0.24 porpoise per kilometer; multiplying this value times the maximum simulated increasing trend yields an upper limit of approximately 0.4 porpoise per kilometer. Less than 5% of all error terms were redrawn in the simulations.

Table 2

Stepwise model selection procedure for 1986–90 aerial survey data. Parameters marked with an asterisk indicate variables included in the model at each step. P = ln(porpoise/km + 0.001); μ = mean value of P; BF = Beaufort sea state; AR = area; CL = cloud cover; YR = year; an × between letters indicates an interaction effect.

STEP Base model	1 $P = \mu$	2 $P = \mu + AR$	3 $P = \mu + AR + CL$	4 $P = \mu + AR + CL + BF$
P-values for tested variables	BF: 0.0587	BF: 0.0079	*BF: 0.0016	YR: 0.8535
	*AR: 0.0001	*CL: 0.0021	YR: 0.5865	BF×AR: 0.8491
	CL: 0.0256	YR: 0.9628	CL×AR: 0.3399	BF×CL: 0.8378
	YR: 0.9258			CL×AR: 0.3875

Results

Survey results

A total of 16,948km of survey effort during 1986–90 resulted in 431 sightings, representing a total of 796 harbor porpoise. The overall mean number of porpoise per kilometer was 0.047. The average values of porpoise per kilometer over the five years are listed in Table 1 for different sighting conditions and areas. Mean group size was 1.85 porpoise, with a range of 1–10 and median 1.

The model

The following model provided the best fit to the observed logarithmic estimates of porpoise per kilometer:

$$P = \mu + \alpha_{Bi} + \alpha_{Cj} + \alpha_{Ak} + \varepsilon_{i,j,k} \qquad (2)$$

where P = $\log_e$ of [(porpoise/km) + 0.001],
μ = mean value of P,
α_{Bi} = effect of Beaufort sea state i on P,
α_{Cj} = effect of cloud cover j on P,
α_{Ak} = effect of area k on P,
$\varepsilon_{i,j,k}$ = normally distributed error with a mean of zero.

The model selection procedure is outlined in Table 2. None of the included variables lost significance and subsequently had to be dropped after inclusion of other variables. The yearly trend was not significant, so the model is essentially reduced to an analysis of variance (ANOVA) model. The results of the complete ANCOVA model testing for a yearly trend in the 1986–90 harbor porpoise data are shown in Table 3. The effects of area, cloud cover, and Beaufort sea state were significant ($P<0.0001$, $P<0.0006$, and $P<0.0021$, respectively), the yearly trend was not ($P = 0.8535$). None of the interaction effects were significant. The parameter estimates for the models with and without year are displayed in Table 4.

Table 3

Results of the weighted analysis of covariance.

Source	df	Sum of squares	Mean square	F value	Prob. >F
Model	5	15397	3079	10.46	0.0001
Area	1	9494	9494	32.24	0.0001
Cloud cover	1	3927	3927	13.34	0.0006
Beaufort	2	4095	2047	6.95	0.0021
Year	1	10	10	0.03	0.8535
Error	54	15900	294		

Table 4

Parameter estimates from (A) the ANCOVA testing year, and (B) the 'best' model (ANOVA) chosen for the simulations. Standard errors are given in parentheses.

	Parameter	(A)		(B)	
μ	Mean	−2.1496	(0.3288)	−2.1454	(0.3251)
α_{B1}	Beaufort 0&1	0.0000	—	0.0000	—
α_{B2}	Beaufort 2	−0.0838	(0.3304)	−0.0883	(0.3266)
α_{B3}	Beaufort 3	−1.1344	(0.3516)	−1.1257	(0.3453)
α_{A1}	Area 1 (South)	−1.5338	(0.2701)	−1.5360	(0.2674)
α_{A2}	Area 2 (North)	0.0000	—	0.0000	—
α_{C1}	Clear skies	0.0000	—	0.0000	—
α_{C2}	Cloudy skies	−1.0377	(0.2841)	−1.0454	(0.2787)
δ	Year	+0.0182	(0.0982)	—	—

Analysis of power to detect trends

No trend simulations ($\delta = 0$) To determine the reliability of the simulation procedure to model trends in porpoise abundance, 500 simulated data sets with no yearly trend were created for five, six, eight, and ten survey years, using parameter set (B) in Table 4. The simulated data sets were analyzed using the full

Table 5

Actual α-errors and fractions of positive and negative covariate coefficient estimates (δ) for ANCOVA of 500 random data sets for five, six, eight, and ten simulated survey years.

No. of years	% annual change	Actual α-errors for			Fractions of ± δ values
		$\alpha = 0.05$	$\alpha = 0.10$	$\alpha = 0.20$	
5	none	0.05	0.10	0.20	0.48/0.52
6	none	0.06	0.11	0.21	0.54/0.46
8	none	0.04	0.10	0.20	0.49/0.51
10	none	0.07	0.12	0.23	0.53/0.47

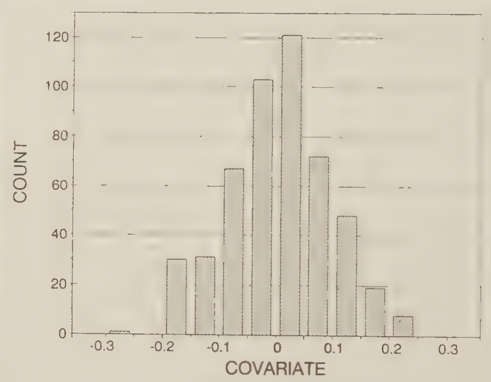

Figure 4

Distribution of covariate estimates (δ) representing yearly change in abundance of harbor porpoise (from ANCOVA) for 500 simulations of five survey years with no annual trend in abundance.

ANCOVA model with a null hypothesis of no trend in abundance. The α-error (Type I error) is the fraction of simulations which falsely detected a trend.

For all four simulations, the resulting α-errors were close to the theoretical ones (Table 5). The average root mean-square-error term obtained for these data sets (16.63) was also close to the error for the actual data (17.01). The estimates of the covariate for year (δ) in the simulated data were approximately normally distributed with a zero mean, as expected (Fig. 4). This confirms that the simulation procedures do not introduce substantial bias into the data or error structure.

Simulations with trends ($\delta \neq 0$) To analyze the power of this procedure to detect given trends, random data sets spanning five, six, eight, and ten years were created with artificial changes in abundance of ±5% and ±10% per year. All other parameters were taken from Table 4, set (B), as above. For each combination of survey years and trend, 500 data sets were created and analyzed with the ANCOVA procedure.

In each simulation, a fraction of the analyses did not detect a trend: this represents the β-error (Type II error). A much smaller fraction detected a trend in the opposite direction of the true trend. The latter presents a special case (dilemma), and we have termed this type of error γ-error (Type III, cf. Carmer 1976). Figure 5 graphically illustrates α, β, and γ for a situation where an increasing trend is occurring and being tested against the null hypothesis in a two-tailed test (in a one-tailed test, γ is zero). The three types of errors are interdependent: as α increases (i.e., the bars in Figure 5 move closer to zero), β decreases, and γ increases.

Power has been defined as the probability of correctly rejecting the null hypothesis when it is false, which numerically is $1-\beta$ (Rotenberry and Wiens 1985, Peterman 1990ab). However, this definition does not address the error associated with accepting a false alternate hypothesis (γ). In the case of trend analysis, this is the probability of rejecting the null hypothesis (no trend) in favor of a trend in the wrong direction. We therefore suggest that power be defined more precisely to include only the probability of detecting the correct alternate hypothesis, which numerically is $1-(\beta+\gamma)$.

Using this definition, the power to correctly detect trends in harbor porpoise abundance is displayed in Table 6 for six different levels of α. The values listed under $\alpha = 1.0$ correspond to the fraction of the time that the sign of the covariate is correct, regardless of significance level. At this α-level, the β-error is zero, because the null hypothesis of no trend is always rejected in favor of either an increasing or a decreasing trend. Both power and γ-errors are maximized when $\alpha = 1.0$ (see Discussion below).

At $\alpha = 0.05$, the ability to detect trends in abundance of harbor porpoise is poor (0.07–0.79) for all tested trends and numbers of survey years. This is below the level of power = 0.80 which has been suggested as a minimum standard (Skalski and McKenzie 1982, Peterman and Bradford 1987). Raising α-levels improves the ability to detect trends, but also increases the chance of detecting a trend in the opposite direction of the true trend (γ-error). When $\alpha = 0.05$, γ-errors are less than 0.01 for the levels of change tested. In contrast, at $\alpha = 0.20$, γ-errors range from 0 to 0.05, and with $\alpha = 1.0$, γ-errors are between 0 and 0.33. Both β and γ-errors are reduced with larger trends and more survey years.

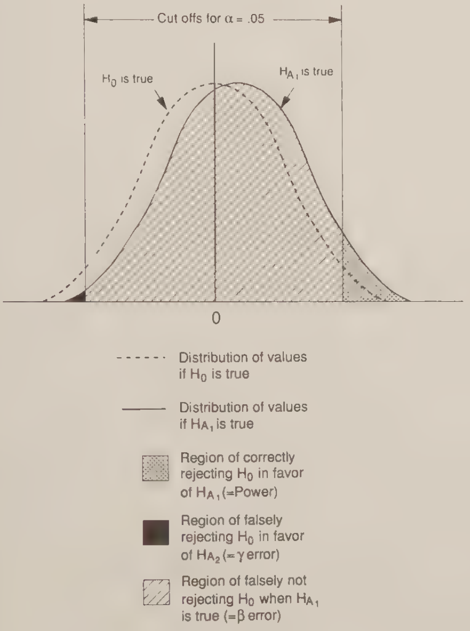
Cut offs for α = .05
H_0 is true
H_{A_1} is true
0
Distribution of values if H_0 is true
Distribution of values if H_{A_1} is true
Region of correctly rejecting H_0 in favor of H_{A_1} (=Power)
Region of falsely rejecting H_0 in favor of H_{A_2} (=γ error)
Region of falsely not rejecting H_0 when H_{A_1} is true (=β error)

Figure 5

Graphic illustration of the errors associated with a two-tailed test, such as trend analysis. Solid line represents the distribution of coefficients for a hypothetical increasing trend. Dashed line represents the null distribution of coefficients (when there is no trend). Shaded areas represent the three error types, α, β, and γ (see text). H_{A1} represents an increasing trend, H_{A2} represents a decreasing trend, and H_0 represents no trend.

Table 6

Estimated power of the analysis to detect a given trend in harbor porpoise abundance correctly, based on 500 random data sets for each combination of change and number of survey years. Power is defined as $1-(\beta+\gamma)$.

No. of years	% annual change	Power associated with given α-error α = 0.05	0.10	0.20	0.30	0.40	1.0
5	−10	0.17	0.24	0.36	0.43	0.52	0.82
6	−10	0.23	0.35	0.52	0.60	0.68	0.90
8	−10	0.52	0.63	0.74	0.82	0.86	0.98
10	−10	0.79	0.87	0.92	0.95	0.97	1.00
5	+10	0.11	0.18	0.29	0.39	0.47	0.78
6	+10	0.21	0.32	0.45	0.54	0.63	0.89
8	+10	0.46	0.56	0.70	0.80	0.85	0.97
10	+10	0.74	0.82	0.88	0.93	0.96	1.00
5	−5	0.08	0.14	0.22	0.28	0.35	0.70
6	−5	0.10	0.16	0.29	0.38	0.44	0.72
8	−5	0.17	0.27	0.42	0.50	0.59	0.84
10	−5	0.27	0.37	0.55	0.65	0.71	0.91
5	+5	0.07	0.13	0.20	0.27	0.34	0.67
6	+5	0.10	0.16	0.25	0.34	0.40	0.73
8	+5	0.15	0.23	0.35	0.45	0.53	0.83
10	+5	0.25	0.34	0.48	0.57	0.66	0.89

Discussion

The number of years necessary to detect trends in harbor porpoise abundance with the techniques described above will depend on two things: the rate of change to be detected, and the degree of certainty desired. A 5% annual change will be more difficult to detect than a 10% change over the same time period. If a large change must occur before the trend is detected, such methods may be of limited use in the management of populations, and more powerful techniques may be required.

If one does not need the ability to determine both increases and decreases, but merely wishes to determine whether a population is declining (objective 3, Peterman and Bradford 1987), one-tailed statistical tests can be used and will increase statistical power. Alternatively, if one is willing to accept a larger probability of inferring a trend when none is actually present, the power to detect trends can be improved by raising the level of α used to determine statistical significance.

It has been suggested that appropriate levels for α and β should be determined based on the relative costs of committing each type of error (Toft and Shea 1983, Rotenberry and Wiens 1985, Hayes 1987, Peterman 1990b). If the cost of failing to detect a change in abundance is high relative to the cost of falsely detecting a trend for a stable population, then the traditional α-level of 0.05 may be inappropriate. In such cases it may be preferable to minimize β-errors by increasing α. For example, in the context of ecological monitoring, Hinds (1984) suggests that α should be made equal to β. However, it is important to remember that increasing α when power is low also raises γ from virtually zero to potentially large levels. Rather than equalizing α and β, a tradeoff must be made between all three types of error. The magnitude of these errors can be estimated using simulations.

When α is raised to 0.10, ten years of data are sufficient to yield power greater than 0.80 and a γ-error of virtually zero when a 10% annual change is occurring. However, this corresponds to a very large total change in abundance (236% increase or 61% decrease). A smaller, but still substantial, change of 5% per year (total 155% increase or 37% decrease) would have a very low chance of being detected at this level of α. If small changes are to be detected, then α may have to be set higher.

The most extreme form of raising α-levels is accomplished by considering only the sign of the estimate for the covariate coefficient in the ANCOVA, thus setting $\alpha = 1$. In this case, the direction, rather than the presence, of a trend is tested for. This approach maximizes power, and may be an alternative for situations where power cannot be improved through other means (i.e., increasing the number of surveys conducted). For harbor porpoise trend estimation, the roughly equal fractions of positive and negative covariate coefficient estimates, $\hat{\delta}$ (Table 5) indicate that such an analysis is not biased towards detecting either trend direction.

With $\alpha = 1.0$, power to detect the correct trend in harbor porpoise abundance ranges from 0.67 to 1.00 for 5–10 survey years and ±5% and ±10% annual population changes. Power of 0.80 or higher is achieved with $\alpha = 1.0$ after 5–6 survey years for a 10% annual change, or after 8 survey years for a 5% annual change. However, since the cost of low power in this case is a γ-error, power should be higher than when α is set at the traditional level of 0.05. In this case, eight survey years may provide high enough power to detect an annual 10% change, whereas even 10 years may not yield sufficient power to detect the smaller 5% annual change.

The magnitude of the γ-error when $\alpha = 1.0$ can be demonstrated with Figures 6 and 7. The three curves in these figures represent the distribution of covariate coefficients, $\hat{\delta}$, for 500 simulated data sets with annual changes of (A) −10%, (B) 0%, and (C) +10%. The γ-error is represented by the area under curves A and C which lies on the incorrect side of zero. If this area is small or equal to zero, as when 10 annual surveys are conducted (Fig. 6), then the analysis will have a high probability of detecting the direction of a trend correctly. However, if the area is large, as when only five annual surveys are conducted (Fig. 7), then the procedure will not be able to detect the direction of trends accurately. The large degree of overlap between the three curves in Figure 7 also reflects the low power to detect trends. The dotted line marks the location of the covariate coefficient estimate ($\hat{\delta}$) for the 1986–90 survey data. It is apparent that the estimate could reasonably come from any of the three distributions.

Setting $\alpha = 1.0$ is valid only if the costs of interpreting a nonexistent trend in a stable population are small in relation to the costs of failing to detect an existing trend. This may be the case if one needs to determine whether an existing level of take from a commercially exploited population is sustainable. The cost of not detecting a decreasing trend could be extinction of the population and the permanent loss of a resource. On the other hand, eliminating or reducing exploitation on a stable population which is incorrectly thought to be decreasing would cause smaller, short-term costs. In the case of marine mammals in the United States, existing laws mandate that all species be maintained at sustainable levels, so extinction represents an unacceptably high cost.

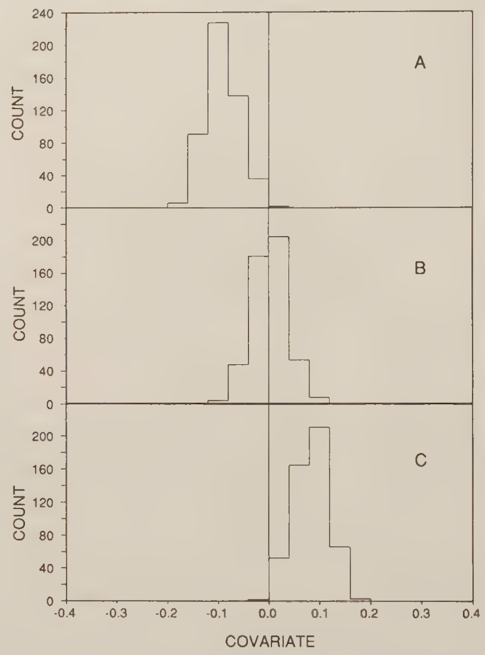

Figure 6

Distribution of covariate estimates ($\hat{\delta}$) representing yearly change in abundance (from ANCOVA) for 500 simulations each of (A) 10% annual decrease, (B) no change, and (C) 10% annual increase in abundance over 10 survey years. Shaded area under curves A and C which lies on the incorrect side of zero represents the γ-error when $\alpha = 1.0$; here, it is essentially zero.

Several assumptions of the above procedures must be discussed. The most critical assumption is that the five years of data collected during 1986–90 characterize the level of variability expected in a longer time series. In addition, the results of the simulations are only accurate if the ANCOVA model is appropriate. The results indicate that the chosen model fits the data well ($P<0.0001$).

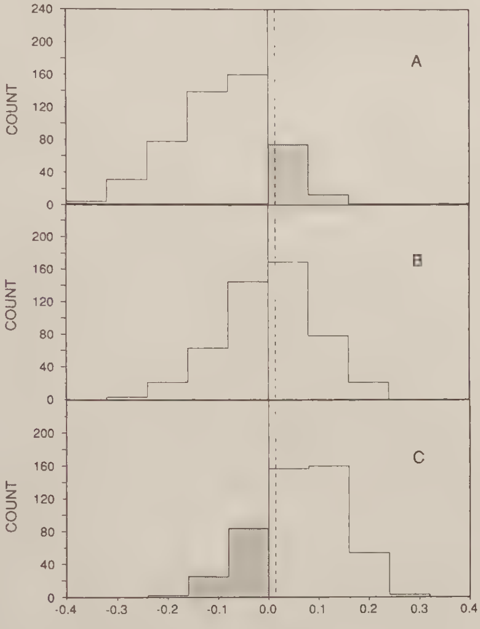

Figure 7

Distribution of covariate estimates ($\hat{d}$) representing yearly change in abundance (from ANCOVA) for 500 simulations each of (A) 10% annual decrease, (B) no change, and (C) 10% annual increase in abundance over five survey years. Shaded area under curves A and C which lies on the incorrect side of zero represents the γ-error when $\alpha = 1.0$. Dashed line marks location along the x-axis of the covariate estimate for actual 1986–90 harbor porpoise data.

The choice of adding the constant 0.001 in the log-transform may at first seem a bit odd, but in fact would be the same as the more familiar transformation $\ln(x + 1)$ if relative abundance had been defined as porpoise per thousand kilometers, rather than porpoise per kilometer. Several other constants were tested to determine if the choice of transformation might influence the analysis. The stepwise procedure yielded the same model in each case. The value 0.001 was chosen because it yielded the most normal distribution of porpoise per kilometer values (Fig. 3B).

This approach to trend analysis also assumes that the fraction of animals visible from the air does not change over time. The probability of detection can be influenced by many factors, particularly sighting conditions, porpoise behavior and group sizes, and observer differences. In our analysis, we controlled for sighting conditions by eliminating poor conditions and stratifying by the remaining ones. Changes in observers between years prevented tests of observer differences. However, based on previous tests with three years of data, they are not believed to be significant (Forney et al. 1989).

Harbor porpoise behavior, including frequencies of active versus inactive behaviors and mean group sizes, has been shown to vary by area and season (Calambokidis et al. 1990, Taylor and Dawson 1984, Sekiguchi 1987). To control for these potential differences, the surveys followed the same transect lines during the same season (autumn) each year. Nevertheless, group sizes in 1989 were significantly different than those in 1987 and 1988 (Kolmogorov-Smirnov test of cumulative distributions, $P = 0.02$ for both tests). The difference appears to be due to a larger percentage of groups containing three or more animals.

If group size affects harbor porpoise sightability, a substantial change in group size distribution could bias the trend analysis, either obscuring a present trend or creating a false one. To test for this possibility, the ANCOVA was repeated excluding the data for 1989. The overall results were similar, with the same final model, similar parameters, and no significant yearly trend ($P = 0.98$). We conclude that this slight difference in group sizes is not likely to have affected our analysis.

Conclusion

The use of simulations allows researchers to estimate appropriate error levels for the analysis of surveys of animal populations. The ANCOVA model we used suggests that no trend in harbor porpoise abundance occurred between 1986 and 1990. However, our simulations show that the power of this model to detect trends using conventional α-levels of 0.05 or 0.10 is poor. Therefore, it is more correct to say that we could not reject the null hypothesis of no trend due to insufficient power.

Power can be increased by raising the acceptable level of α. If only the sign of the coefficient for the covariate year is used to determine the direction of a trend, regardless of significance level, then the ANCOVA has a high probability of detecting trends correctly, particularly with eight or more annual surveys. However, at higher α levels, the probability of detecting a change in the wrong direction (γ-error) increases.

When making decisions, there are distinct trade-offs between the error types which must be evaluated. In trend analysis, power should be defined as $1 - (\beta + \gamma)$ to include only detection of a trend in the correct direction. If the cost of making an α-error, i.e., falsely concluding that a stable population is increasing or decreasing, is low, α can be increased to increase power. However, attention must be paid to both β and γ-errors as power increases. If γ is relatively large, then power should be greater than the previously suggested value of 0.80.

Additional surveys improve the power to detect trends and reduce γ-errors. Furthermore, if future research can identify and record additional factors affecting observed abundances, such as productivity of the area surveyed (Smith et al. 1986) or ocean temperature patterns (Reilly 1990), this may reduce the variability in the model and increase power.

Future research is planned to continue surveys and search for alternative methods of analyzing these data. The traditional approach to making statistical inference regarding trends has been hypothesis testing with a null hypothesis of no change. As seen in this paper, this is a complicated approach. One must first decide what levels of α, β, and (now) γ one is willing to tolerate. The range of these errors is dependent on many factors, including the level of change to be detected, and the number of years surveyed. Once inference is made, it cannot be presented to others without reference to this bewildering array of decision criteria.

Bayesian statistics (Iversen 1984, Press 1989) may offer an alternative approach to statistical inference, circumventing many of the complications discussed above. Bayesian methods would allow the calculation of the probability distribution of possible trends given the observed data. From this distribution it would be possible to directly calculate the probability that the population is increasing or decreasing. Such methods may be of more value than statistical test results which are highly dependent on the chosen error levels.

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Citations

Barlow, J.
1987 An assessment of the status of harbor porpoise populations in central California. Admin. Rep. LJ-87-06, Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, P.O. Box 271, La Jolla, CA 92038, 34 p.
1988 Harbor porpoise (*Phocoena phocoena*) abundance estimation in California, Oregon and Washington: I. Ship surveys. Fish. Bull., U.S. 86:417–432.

Barlow, J., and D.A. Hanan
1990 An assessment of the status of harbor porpoise populations in California. Working Paper SC/42/SM6 presented to the IWC Scientific Committee, June 1990 (unpubl.). Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, P.O. Box 271, La Jolla, CA 92038, 31 p.

Barlow, J., C. Oliver, T.D. Jackson, and B.L. Taylor
1988 Harbor porpoise (*Phocoena phocoena*) abundance estimation in California, Oregon and Washington: II. Aerial surveys. Fish. Bull., U.S. 86:433–444.

Calambokidis, J., C. Ewald, G.H. Steiger, S.M. Cooper, I.D. Szczepaniak, and M.A. Webber
1990 Harbor porpoise studies in the Gulf of the Farallones. Final report for contract CX 8000-8-0001 to Gulf of Farallones Natl. Mar. Sanctuary, NOAA, San Francisco, by Cascadia Research Collective, Olympia, WA 98501, 57 p.

Carmer, S.G.
1976 Optimal significance levels for application of the least significant difference in crop performance trials. Crop Sci. 16:95–99.

Diamond, S.L., and D.A. Hanan
1986 An estimate of harbor porpoise mortality in California set net fisheries, April 1, 1983 through March 31, 1984. Admin. Rep. SWR-86-15, Southwest Region, Natl. Mar. Fish. Serv., NOAA, 300 S. Ferry Street, Terminal Island, CA 90731, 40 p.

Forney, K.A., D.A. Hanan, and J. Barlow
1989 Detecting trends in harbor porpoise abundance using aerial surveys: A preliminary report based on three years. Admin. Rep. LJ-89-20, Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, P.O. Box 271, La Jolla, CA 92038, 18 p.

Hanan, D.A., S.L. Diamond, and J.P. Scholl
1986 An estimate of harbor porpoise mortality in California set net fisheries, April 1, 1984 through March 31, 1985. Admin. Rep. SWR-86-16, Southwest Region, Natl. Mar. Fish. Serv., NOAA, 300 S. Ferry Street, Terminal Island, CA 90731, 38 p.
1987 An estimate of harbor porpoise mortality in California set net fisheries, April 1, 1985 through March 31, 1986. Admin. Rep. SWR-87-5, Southwest Region, Natl. Mar. Fish. Serv., NOAA, 300 S. Ferry Street, Terminal Island, CA 90731, 9 p.

Hayes, J.P.
1987 The positive approach to negative results in toxicology studies. Ecotoxicol. Environ. Saf. 14:73–77.

Hinds, W.T.
1984 Towards monitoring of long-term trends in terrestrial ecosystems. Environ. Conserv. 11:11–18.

Iversen, G.R.
1984 Bayesian statistical inference. Sage University paper on quantitative applications in the social sciences, 07-043. Sage Publ., Beverly Hills, CA.

Joyner, S.P. (editor)
1985 SAS/STAT guide for personal computers, Version 6 edition. SAS Inst. Inc., Box 8000, Cary, NC 27511-8000.

Peterman, R.M.
1990a Statistical power analysis can improve fisheries research and management. Can. J. Fish. Aquat. Sci. 47:2–15.
1990b Comment on forest decline and acidic deposition: The importance of reporting statistical power. Ecology 71: 2024–2027.

Peterman, R.M., and M.J. Bradford
1987 Statistical power of trends in fish abundance. Can. J. Fish. Aquat. Sci. 44:1879–1889.

Press, S.J.
1989 Bayesian statistics: Principles, models and applications. John Wiley & Sons, NY, 237 p.

Reilly, S.B.
1990 Seasonal changes in distribution and habitat differences among dolphins in the eastern tropical Pacific. Mar. Ecol. Prog. Ser. 66:1–11.

Rotenberry, J.T., and J.A. Wiens
1985 Statistical power analysis and community-wide patterns. Am. Nat. 125:164–168.

Sekiguchi, K.
1987 Occurrence and behavior of harbor porpoises (*Phocoena phocoena*) at Pajaro Dunes, Monterey Bay, California. M.S. thesis, San Jose State Univ., San Jose, CA, 36 p.

Skalski, J.R., and D.H. McKenzie
1982 A design for aquatic monitoring programs. J. Environ. Manage. 14:237–251.

Smith, R.C., P. Dustan, D. Au, K.S. Baker, and E.A. Dunlap
1986 Distribution of cetaceans and sea-surface chlorophyll concentrations in the California Current. Mar. Biol. 91:385–402.

Taylor, B., and P.K. Dawson
1984 Seasonal changes in density and behavior of harbor porpoise (*Phocoena phocoena*) affecting census methodology in Glacier Bay National Park, Alaska. Rep. Int. Whaling Comm. 34:479–483.

Toft, C.A., and P.J. Shea
1983 Detecting community-wide patterns: Estimating power strengthens statistical inference. Am. Nat. 122:618–625.

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American Journal of Primatology 23:127–135 (1991)

TECHNICAL NOTE

A Bar Code Scoring System for Behavioral Research

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A data collection method using lap-top computers and bar codes was developed and used in behavioral research. The studies involved several common sampling methods and a variety of study subjects. Advantages and restrictions of the system are discussed. Overall, we found bar code technology to increase both efficiency and accuracy of behavioral data collection.

Key words: portable computer, behavior, data collection

INTRODUCTION

In the past two decades, there has been a gradual progression in behavioral research away from checksheets towards event recorders and portable computers. Unfamiliarity with computers and a reluctance to abandon proven methods have often prevented researchers from adopting such newer methods. However, if these obstacles can be overcome, the advantages of computerized systems are well worth the effort. They include increased efficiency of data collection and analysis, more rapid transfer to permanent data bases, reduction of transcription errors, reduced volume of archived records and decreased data handling time [Flowers & Leger, 1982; Cooney, 1985; Unwin & Martin, 1987].

Bar codes have become a familiar part of our environment. They are used effectively in sales, inventory, manufacturing, and other applications where large amounts of information must be processed. Bar codes provide an easy and accurate means of data entry with minimal observer training and computer programming requirements. We have applied this technology to behavioral research, utilizing a variety of sampling methods and portable TRS-80 Model 100 and 102 computers. This article describes how we applied bar code technology and discusses advantages and restrictions of its use in behavioral research.

METHODS

Bar Codes

Bar code technology as described in Talbott & Parliman [1987] involves four major components: a bar code symbol, comprised of black lines and spaces of varying widths; a scanning device; a decoder; and a computer to process the coded

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information. In the bar code, alphanumeric characters and certain punctuation symbols are represented by specific sequences of lines and spaces. The individual components can be combined into words, numbers, or other meaningful expressions. The scanning device reads the bar code with an infrared sensor. Decoding software installed on the data entry computer translates the pattern into the original characters for subsequent processing and storage.

Hardware

In our study, we used the TRS-80 Model 100 lap-top computer and its successor, the Model 102 [Hensler et al., 1986]. To provide additional space for data, the memory on each computer was expanded to 32 kilobytes. A cassette recorder with EAR, AUX, and REM ports and a computer cassette interface cable were required to install the bar code decoding software onto the portable computer. The scanning device was a detachable TRS-80 digital wand. Data storage and analysis were carried out on Apple Macintosh Plus and SE microcomputers. A Hayes compatible modem cable with a null modem adapter enabled transfer of data directly from the portable TRS-80 to the Macintosh. High resolution bar codes were generated with a laser printer and placed under protective, self-adhesive photo album sheets.

Software

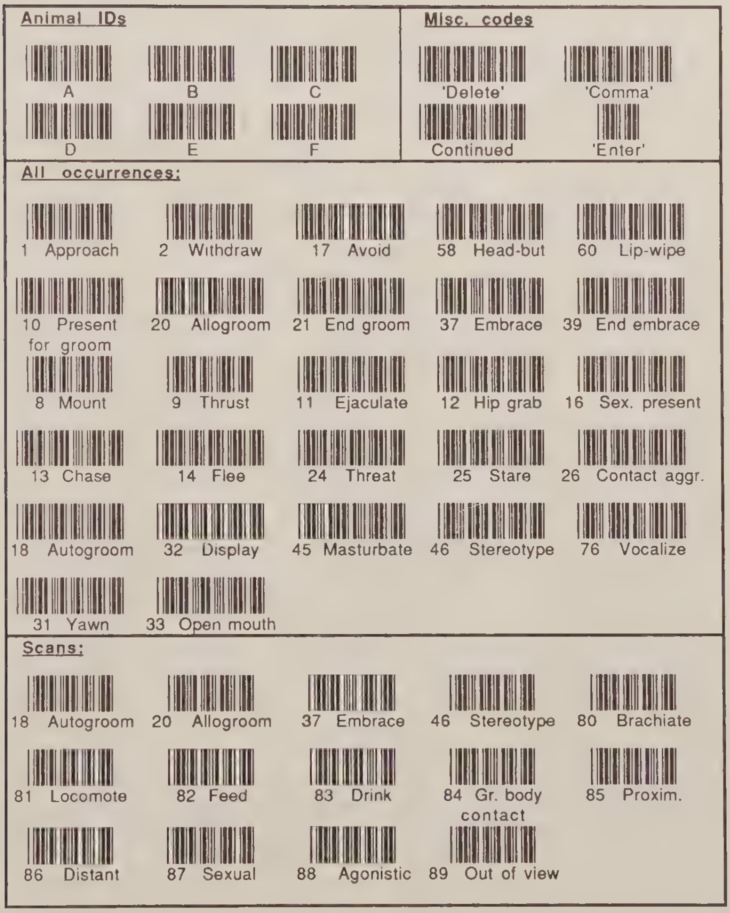
Many kinds of software applications are available to create bar codes on different computer systems. A flexible and simple system for the Macintosh was obtained through installation of a 'bar code' font into the system file. This approach allows any word processing software to produce documents containing bar codes. Software which enables the portable TRS-80 to decode bar codes was included with the scanner. Communications software was only necessary for the personal computer, as the TRS-80 has its own built-in program. A structured BASIC programming language on the Macintosh facilitated data processing and analysis.

Programs and Sampling Methods

We developed BASIC programs on the protable TRS-80 for two types of focal animal data collection (one-zero sampling and timed behaviors), and for a widely used combination of focal animal and periodic instantaneous or scan sampling (terminology follows Altmann [1974]). A variety of prompts, checks, and auditory cues were included in these programs to assist the user, facilitate data entry, and reduce errors in data collection. All programs provided a limited ability to correct errors while collecting data. Some of the programs allowed the observer to add notes at the end of the observation. The portable TRS-80's internal clock was used to determine times, as needed for each study. The study subjects were mainly primates, but also included cheetahs, elephants, and condors (see Fig. 1 for a sample bar code ethogram).

For all data collection methods, we chose to create detailed data files containing header information and data in raw or partially processed form (see Fig. 2 for a sample data file). This provided the most complete data files, and made them easier to understand, because they resembled traditional data collection forms. The files were later reformatted for analysis with a program on the microcomputer.

The programs designed for the collection of sequential focal animal data combined with scans were made as flexible as possible, allowing for virtually any format of sequential behaviors, including simultaneous or overlapping behaviors (e.g., ACTOR-BEHAVIOR-RECIPIENT, . . . or BEHAVIOR1, BEHAVIOR2, BEHAVIOR1-C, . . . where C indicates a continued behavior). The end of an interval was recorded with a specific bar code. The programs automatically prompted



Animal IDs

A B C
D E F

Misc. codes

'Delete' 'Comma'
Continued 'Enter'

All occurrences:

1 Approach
2 Withdraw
17 Avoid
58 Head-but
60 Lip-wipe
10 Present for groom
20 Allogroom
21 End groom
37 Embrace
39 End embrace
8 Mount
9 Thrust
11 Ejaculate
12 Hip grab
16 Sex. present
13 Chase
14 Flee
24 Threat
25 Stare
26 Contact aggr.
18 Autogroom
32 Display
45 Masturbate
46 Stereotype
76 Vocalize
31 Yawn
33 Open mouth

Scans:

18 Autogroom
20 Allogroom
37 Embrace
46 Stereotype
80 Brachiate
81 Locomote
82 Feed
83 Drink
84 Gr. body contact
85 Proxim.
86 Distant
87 Sexual
88 Agonistic
89 Out of view

Fig 1. Sample bar code ethogram for the collection of focal animal and group scan data. Animals are identified with a letter code, behaviors have numeric codes.

for scan information when needed, generally at the end of every one or two intervals, as specified when entering header information. The output files contained a header, an interval-by-interval record of behavior sequences, and a table containing scan information. Ad lib notes could be added at the end of the data files.

For the collection of timed focal animal data, the programs were designed to automatically obtain the current time whenever a code was scanned. The start of a new behavior marked the end of the previous one. Individual and cumulative durations were calculated in seconds for all behaviors. The output files contained a header, a table of durations for each behavior, and optionally an interval-by-interval sequence of behaviors.

Focal animal one-zero sampling was simplified with another type of program. After specifying the interval duration and length of the observation period, the observer scanned each behavior as it occurred. The program automatically scored each behavior only once per appropriate interval, and calculated totals for all behaviors. The output files contained a header and the total number of intervals

```
FOCAL          A
DATE           03/31/89
OBSERVER       EWH
LOCATION       EX
WEATHER        1311
DURATION (M)   10
SCAN INT (S)   60
START TIME     08:15:00

SCANS:
A    B
-------
86   86
86   86
20   20
85   85
86   86
87   46
86   46
18   46
86   18
86   86

INTERVALS:
*
A-45-,A-18-,A-21-,B-2-A-,
*

*
B-10-A-,A-1-B-,A-20-B-,
*
CO-,A-21-B-,
*
B-2-A-,
*
A-45-,
*
CO-,
*
A-18-,A-21-,A-18-,
*
CO-,A-21-,A-18-,A-21-,
*

*
<<<END OF OBSERVATION>>>
```

Fig. 2. Sample data file for a combination of focal animal and group scan data. The file is divided into three main sections: header information, scan activity table, and an interval-by-interval record of behaviors for the focal animal. Focal animal data follows the format ACTOR-BEHAVIOR-RECIPIENT. Animals are identified with a letter code, behaviors have numeric codes. Blank intervals indicate that no ethogram behaviors occurred.

during which each behavior occurred. Optionally, it could also print an interval-by-interval table of behaviors that occurred at least once.

RESULTS AND DISCUSSION

Bar code technology enables efficient and accurate data collection, and is adaptable to many research needs. It shares the benefits of other portable com-

TABLE I. Comparison of Efficiency, Accuracy, and Cost of Three Research Methodologies*

	Paper and pencil	Computer with keyboard entry	Computer with bar code entry
Efficiency			
Observer training	Good Memorize behavior codes	Fair Memorize behavior codes learn use of computer	Good Learn use of computer and bar codes
Data processing	Poor Tabulations, data entry	Good Programming, processing	Good Programming, processing
Accuracy			
Timed data	Poor	Good	Good
Correct recording of behavior codes	Fair–Good Observer confuses codes	Fair Observer confuses codes, typographical errors	Good Low probability of confusing codes
Data transcription	Poor	Good	Good
Quality of errors	Frequent, unpredictable, difficult to detect	Some frequent and unpredictable, others rare and systematic	Rare, systematic, easy to detect and correct
Cost			
Equipment	Low	Medium-High	Medium-High
Personnel time (for study preparation)	Low Develop forms	Low-High Develop programs	Low-High Develop programs
Personnel time (for data processing)	High	Low	Low

*The three research methodologies include paper-and-pencil, computerized with keyboard entry, and computerized with bar code entry. Criteria used to evaluate the different methods are listed below the rating.

puter systems and offers additional advantages during data collection. For a more complete comparison with traditional paper-and-pencil methods, we discuss advantages and restrictions specific to bar codes and common to all computerized systems. An overview is presented in Table I.

Advantages

Bar codes primarily increase the efficiency of behavioral data collection. A useful feature is the ability to mask the complexity often present in ethograms. Rather than memorizing numerous codes for behaviors, the observer can rely on brief descriptions next to the bar codes, while the computer stores and processes only the code, keeping data concise (Fig. 1). Because of this, overall training time is generally lower than with paper-and-pencil methods, despite the added task of learning to use the bar code system.

Data are entered more accurately because typographical errors are eliminated and observers are less likely to confuse codes when descriptions are readily available next to the bar codes. In addition, bar code sheets can be customized to enable easy location of behavioral codes. For example, behaviors within a general category (i.e., locomotion) can be grouped, and sections can be separated with lines or different background colors. Light colors, such as those obtained with highlighter

TABLE II. Comparison of Complete Processing Time (in Minutes) Required for 1 Hour of Behavioral Data Collected in a Comprehensive Behavior Study*

Manual data collection and processing		Computerized data collection and processing	
Task	Minutes	Task	Minutes
Prepare for observation	5	Prepare for observation	10
Tabulate/summarize data	10–110	Load data files onto storage and analysis computer	5
Check tabulations	10–25		
Organize forms, make copies	5	Edit and backup data files	2–15
Enter into data base	10–75	Check data files, process with program	3–5
		Verify output and transfer to data base, make backups	3–5
Total processing time	40–220	Total processing time	23–40

*The study addressed aspects of social, breeding, play, and feeding behavior, as well as several other behaviors of interest. The ranges reflect differences in processing time for inactive and active sessions.

pens, are recommended to maintain sufficient contrast between light and dark lines within the bar code.

The number of bar codes that fit on a standard 8.5 × 11 inch sheet of paper depends on the layout of the behavior codes and descriptions, but generally should be on the order of 30–60 bar codes when printed at normal size. Reducing the bar codes to approximately 75% with a laser printer not only increases the number of codes a single sheet can hold (up to 90), but it also makes the codes easier to scan. If more bar codes are necessary, the bar code sheet can be set up with a 'keypad' containing only single digit bar codes, from which the complete codes can be created. For example, the observer would scan 2, then 5 to enter the behavior code 25. Less frequently used codes could be entered in this manner from the keypad to reduce the number of codes required on the bar code sheet.

With some practice, scanning bar codes is faster than writing or typing data, so the observer diverts less attention from the study subject while recording information. This is particularly important when studying active animals, such as primates. Accurate durations can be obtained simply by scanning a bar code which immediately records the time. This feature simplifies data collection and also reduces the incidence of missing times. In our study, we scored only mutually exclusive timed behaviors, but overlapping times could be obtained with a slightly different data entry format.

In general, data collected with a computer can be processed more efficiently than with conventional methods, which often require summarizing information before entry into a computer for analysis and storage. Errors in tabulation and transcription are likely to be introduced. In contrast, if the information is already stored in computer files, this process can be performed more quickly and reliably by a computer program. Transcription errors and manual data entry are essentially eliminated. A comparison of time required to process 1 hour of data in a comprehensive behavioral study which began with paper-and-pencil methodology and later utilized the bar code scoring system is described in Table II. For sessions during which the study animals were relatively inactive, computer processing required approximately half as much time as hand-tabulation. As sessions became more active, this advantage quickly increased to more than a five-fold difference in processing time.

The quality of errors also differs for the two methods: with traditional methods, errors can be introduced during data collection, tabulation, and during entry into a data base for analysis. Such errors are unpredictable and difficult to detect. In comparison, with computerized data collection and analysis, errors are only likely to be introduced while collecting and editing data files. The data tabulation program can include automatic checks for inappropriate information, so these errors may be easily detected. Programming errors could also cause incorrect data tabulation, but such errors are highly systematic and therefore, relatively easy to correct.

A further advantage of computer processing is that, if additional summaries or analyses become necessary at a later time, re-processing computer files requires considerably less time than searching through stacks of data sheets. This is useful in studies where data are collected in more detail than immediately used in analysis, such as when behavioral sequences are obtained, but only frequencies of occurrence or scan data are initially analyzed.

In comparison with the personnel time necessary for manual data processing, a computerized system is also cost-effective. We obtained a complete bar code system using a TRS-80 portable computer for under $600. However, additional funds for development or modification of data entry and processing programs may be required. The amount of time required for this will depend on the complexity of the study, and from our own experience ranges from 2 days to several weeks, with most studies requiring less than 1 week of programming time.

Another key feature is the bar code system's adaptability. From simple to sophisticated data collection requirements, the lap-top computer is easily programmable to meet researchers' needs. After our initial program had been developed for the study of a group of golden monkeys, it was easily modified to meet requirements for studies of other species, including several primates, elephants, cheetahs, and both California and Andean condors. The studies covered a wide range of research interests, including social behavior, chick/juvenile development, feeding patterns, and training responses. As an example, a program developed for the study of cheetah feeding behavior was later modified by a researcher with little previous programming experience for a study of Andean condor chick development.

To facilitate the transition from paper-and-pencil methodology to a computerized system, the programs can be designed to mimic established procedures. Programmable visual and auditory cues allow each data entry program to assist observers and help eliminate common errors. For example, at the end of each required interval, our program buzzed as a reminder to record group scan information, and rejected all inappropriate entries. The format of data files is flexible and easily modified by changing PRINT statements in the program. For rapid analysis, the information can immediately be formatted to meet the specifications of statistical software. If more detail is desired, the data files can be more complex, and a subsequent program can re-format the information for statistical analysis.

Restrictions

We encountered several limitations in using bar codes and portable computers in behavioral research. These problems were minor, and solutions or alternatives were easily implemented, as described below.

When a bar code is successfully scanned, the portable computer emits a beep which acknowledges acceptance of the code. The effect of such tones on the study subject's behavior should be evaluated before using this method of data collection. In our research, some of the study animals were accustomed to noisy environments and did not seem to react. In other cases, observers collected data from within blinds or at a sufficient distance to avoid influencing the animals' behavior.

If the surface of the bar code is not protected, it quickly frays from contact with the scanning device. A thin plastic cover over the bar code sheet prevents this. In general, thin, non-reflective plastics are recommended, as reflections on the plastic can cause erroneous scans. Minimal pressure should be applied while scanning to prevent the plastic itself from being scratched, as this can also interfere with the scanning of the code. Alternatively, scanning devices are available that do not require contact with the bar code surface.

The lap-top computer requires frequent transfer of data to a larger computer, because it is not suitable for long-term data storage. Its small memory restricts the amount of information it can hold. The internal nickel-cadmium battery allows retention of information for only 8–30 days from the time of the last connection to a power source, depending on the amount of memory installed. However, indefinite file storage is possible by maintaining charged batteries in the computer at all times. If used only for file storage, these batteries need infrequent replacing or recharging. When the computer is operated with battery power, battery life is approximately 14–16 hours. However, the use of the digital wand can reduce operating time roughly by half, depending on the number of codes scanned.

Although the lap-top computer can be programmed to produce auditory signals at specified intervals (e.g., for scan sampling), continuous data entry prevents the use of this feature. The auditory time marker can only be activated before and after input is received, so no signal can be produced while the computer is waiting for an entry. We resolved this problem by setting an external time piece to beep at desired intervals.

Finally, the lap-top computer is susceptible to adverse environmental conditions, such as dirt and moisture. A commercially available, molded plastic cover can be affixed to the computer to protect it without inhibiting keyboard use.

CONCLUSIONS

1. The main advantage of applying bar code technology in behavioral research is the increased efficiency and accuracy of data collection.
2. In particular, studies involving durations can benefit from this technology, because accurate times are easy to obtain. Bar code methodology can also facilitate the application of other common data collection methods, such as one-zero sampling, continuous behavior recording, and focal animal or group scans.
3. More rapid analysis is possible than with traditional paper-and-pencil methodology, since the data files are immediately stored on a computer.
4. Bar codes can make it easier to adopt computerized data collection by eliminating many of the problems associated with keyboard entry.
5. The bar code scoring system provides the flexibility to meet many research needs.

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REFERENCES

Altmann, J. Observational study of behavior: sampling methods. BEHAVIOUR 49: 227–265, 1974.

Cooney, T.M. Portable data collectors and how they're becoming useful. JOURNAL OF FORESTRY 83:18–23, 1985.

Flowers, J.H.; Leger, D.W. Personal computers and behavioral observation: an introduction. BEHAVIOR RESEARCH METHODS & INSTRUMENTATION 14:227–230, 1982.

Hensler, G.L.; Klugman, S.S.; Fuller, M.R. Portable microcomputers for field collection of animal behavior data. WILDLIFE SOCIETY BULLETIN 14:189–192, 1986.

Talbott, H.; Parliman, B.J. Using bar code technology for horticultural research and plant inventory activities. HORTSCIENCE 22:359–369, 1987.

Unwin, D.M.; Martin, P. Recording behaviour using a portable microcomputer. BEHAVIOUR 101:87–100, 1987.

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MODELS FOR POWER OF DETECTING TRENDS—A REPLY TO LINK AND HATFIELD

Tim Gerrodette[1]

Link and Hatfield (1990) have criticized the analysis of Gerrodette (1987), which investigated the statistical power of detecting linear or exponential trends in ecological data. The analysis was not limited to detecting temporal changes in the size of animal populations, although to my knowledge it has only been applied in that way; it could also be used, for example, in designing sampling along spatial gradients. Link and Hatfield concluded that the power of detecting a trend had been overestimated by Gerrodette's methods. However, Link and Hatfield's comments do not invalidate the original analysis; rather, they suggest an extension of it. Here I reply to the main points raised by Link and Hatfield, and extend the original results slightly by considering other approaches that relax some of the restrictive assumptions of the 1987 paper.

(1) *Selection of proper statistical distribution.* Gerrodette (1987) employed the standard normal distribution (referred to here as the z distribution) to estimate the power of linear regression analysis to detect trends. Link and Hatfield (1990) argued that the t distribution would be more appropriate to compute power for small sample sizes. The difference arises from considering different statistical models. Link and Hatfield considered the classical regression problem, where the investigator has simply n data points. With no information about the variance of each point, the error variance must be estimated from the deviations of the observed points from the regression line (i.e., from the residual sum of squares). Because a slope and intercept have been computed from the data already, there remain $n - 2$ degrees of freedom (df) for estimating the variance. The measurement of temporal or spatial gradients in ecology may often involve small n (5–10, say), and this means that the t distribution should be used.

In many ecological applications, however, the dependent or response variable (abundance A_i in this case) is not a simple, easily measured quantity. Gerrodette (1987) considered, but did not clearly distinguish, a more complex situation in which estimates of A_i resulted from an extended sampling effort, so that estimates of A_i and also var(A_i) would be made at each of n points. For example, a program to monitor population size, where estimates of A_i and var(A_i) come from annual surveys in year i, would typically produce data of this kind. The df for significance testing may not be clearly defined in this situation, but with reasonably large sampling effort, we may consider that the var(A_i) have been estimated with "large" df. This leads to using the z distribution.

Intermediate cases occur if there are "simple" estimates (i.e., with no associated variance estimates) but with replication or near replication at each "point." With k true replicates at each of n "points," there are $n - 2$ df to test lack-of-fit and $n(k - 1)$ df to estimate true error. If these can be pooled, a total of $kn - 2$ df can be used to estimate variance. Similar considerations apply even if there are not true replicates, but the data can be arranged in n groups of near replicates (not necessarily equal in size) based on values of the independent variable; in such a case there are effectively only n "points" available for fitting the regression line, but a possibly much larger number of values for estimating the error variance.

The general issue is that the degrees of freedom to be used in testing the significance of a regression line are not always simply $n - 2$. Determination of the appropriate df, and hence whether the t or z distribution should be used to estimate power, depends on the nature of the data. One may argue that since the t approaches the z distribution for large df, the t distribution could be used in all cases. In principle this is correct, but there are important practical reasons for using the z distribution when it is suitable. Computational routines are widely available. Indeed, because the z distribution is readily tabled, it is possible to solve many problems, at least approximately, with just a hand calculator. In the original paper (Gerrodette 1987), I attempted to emphasize this practical application. The probability that a trend *will* be detected, given that it is present, is a calculation so infrequently considered that even "quick and dirty" estimates of power will show that many proposed experimental designs have unacceptably low power.

Calculations of power using the t distribution are slightly more involved. For a t test at the α significance level with df degrees of freedom, the power of the test is

$$\Pr\{nct(\mathrm{df},\delta) < t_{\alpha,\mathrm{df}}\}$$

for $\delta < 0$,

$$\Pr\{nct(\mathrm{df},\delta) > t_{1-\alpha,\mathrm{df}}\}$$

for $\delta > 0$, and

---

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$$\Pr\{nct(\mathrm{df},\delta) < t_{\alpha/2,\mathrm{df}}\} + \Pr\{nct(\mathrm{df},\delta) > t_{1-\alpha/2,\mathrm{df}}\}$$

in the two-sided case, where δ is the noncentrality parameter of the noncentral t distribution *nct*. Unfortunately, Link and Hatfield (1990) tried to use the central t distribution to compute power, and thus incorrectly concluded that power could only be estimated by Monte Carlo simulation. Tables of the noncentral t distribution are available (Resnikoff and Lieberman 1957, Owen 1965, Park 1972), but the function is more easily implemented by computer routines in IMSL (function TNDF), SAS (function PROBT), and some specialized programs for computing power (Goldstein 1989).

In the present case, the noncentrality parameter δ is equal to

$$\delta = \frac{b}{\sigma_b},$$

where b is the true slope of the regression line. Note the similarity of this formula with the usual test statistic for the regression line

$$T = \frac{\hat{b}}{s_{\hat{b}}}.$$

The test statistic T, however, uses estimates for the slope of the regression line and its standard deviation derived from the data. A calculation of power, on the other hand, is conditional on specified population values, not sample estimates, a point sometimes confused.

Note also that δ as defined above is a dimensionless number that measures the difference of the slope of the regression line from the null hypothesis H_0: $b = 0$ in standardized units. For this reason, δ can be thought of as a measure of the strength of some effect one is trying to detect through the regression analysis, i.e., an effect size index (Cohen 1988).

To sum up, using the z distribution to calculate power is a valid approach if the number of df is effectively "large." If the number of df is "small," particularly in the classical regression case with $n - 2$ df, the t distribution will provide more accurate estimates of power. Because t values are larger than corresponding z values for any finite df, calculations of power based on the t distribution will always be lower than those based on the z distribution. Similarly, calculations based on the t distribution will indicate higher rates of change needed to be detectable, as well as larger sample sizes and smaller coefficients of variation needed to detect a given rate of change. The numerical difference between calculations of power using the z and t distributions may or may not be important, depending on several factors in addition to df (factors discussed in Gerrodette 1987). A specific example is shown in Fig. 1 with $n = 10$, $\alpha = .05$, for the linear model with the coefficient of variation (cv) proportional to the inverse of the square root of abundance (see Gerrodette 1987), with power plotted as a function of the rate of change.

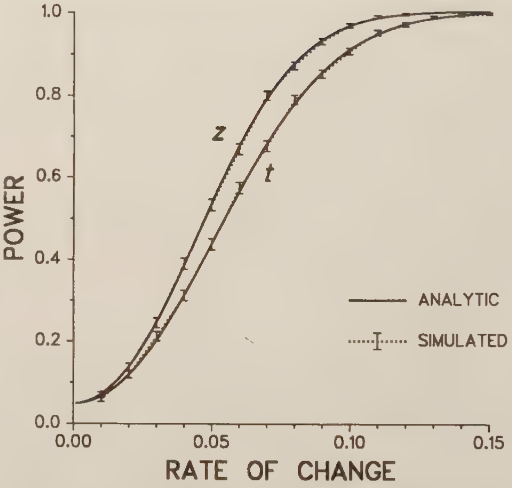

FIG. 1. Power of linear regression as a function of r, the rate of change, estimated by analytic formula and Monte Carlo simulation, and based on either the z or t distribution. Calculations are based on the linear model with cv $\propto A^{-1/2}$, $\mathrm{cv}_1 = 0.2$, $n = 10$, and $\alpha = .05$, two-tailed (cf. Gerrodette 1987). The simulation results are so close to the analytic results that they are difficult to distinguish. Error bars show 95% binomial confidence intervals for 5000 simulations.

(2) *Accuracy of analytic results.* The models considered in Gerrodette (1987) involved violations, to various degrees, of the normal and homoscedastic assumptions of linear regression. These violations were explicitly recognized in the original paper. Because of such violations, the formulae presented did not compute power exactly, but only estimated, or approximated, power. Link and Hatfield (1990) have confirmed this, showing that the formulae are not exact. The question remains, however, whether the approximations are sufficiently accurate to be useful in practice in an experimental design context. Both simulations (discussed in the next paragraph) and analytic comparison (Appendix) show that they are.

Link and Hatfield (1990) claimed that analytic estimates of power for the models discussed in Gerrodette (1987), even if based on the t distribution, were invalid, and they recommended Monte Carlo simulations. However, Link and Hatfield's calculations of power were invalid because they were based on the central t distribution, rather than the noncentral t, as noted in the previous section. I used simulations to verify the original analytic results, but did not report the simulations at that time. Simulation results using either the z or t distribution generally agree with analytic formulae within the uncertainty of the Monte Carlo estimator (Fig. 1). Data for each run of the Monte Carlo simulations were randomly drawn from normal distributions with means A_i and variances var(A_i) as given in Gerrodette (1987). Analytic values of power in Fig. 1 were computed with either the z or t distribution functions using $\delta = b/\sigma_b$, where b and σ_b were computed from equations in Gerrodette (1987). The close agreement of the analytic formulae with the simulations, in spite of known violations of assumptions of the regression model, is probably due to two factors: linear regression is a robust procedure, and the change in abundance is small (on a relative basis) in typical trend problems.

Therefore, the supposed overestimation of power that Link and Hatfield (1990) discussed is not due to any problem with the analysis presented in Gerrodette (1987), but relates entirely to a different model based on the t distribution. Link and Hatfield's simulation results ("actual" in their figures) are indistinguishable from the results, simulated or analytic, based on the t distribution properly computed (compare Fig. 1 with their Fig. 1). Furthermore, their simulated estimate of power for the sea otter (*Enhydra lutris*) example (Gerrodette 1987: 1368–1370) is virtually identical to the analytic calculation of power using the t distribution (0.424 vs. 0.420). Monte Carlo simulation is certainly a useful tool, and could profitably be used in situations less tractable than the simple models of my original paper. For linear (additive) and exponential (multiplicative) models of change with equally spaced sampling, however, the analytic approximations are quite adequate, and simulations are unnecessary.

(3) *More general approaches.* The analysis of Gerrodette (1987) was based on unweighted linear regression with equal sampling effort at equally spaced points. These are fairly restrictive assumptions. More generally, the slope and variance of a weighted regression line, using the inverse of the point variances $V_i = \mathrm{var}(A_i)$ as weights, are

$$b = \frac{\sum \frac{1}{V_i} \sum \frac{x_i A_i}{V_i} - \sum \frac{x_i}{V_i} \sum \frac{A_i}{V_i}}{\sum \frac{1}{V_i} \sum \frac{x_i^2}{V_i} - \left(\sum \frac{x_i}{V_i}\right)^2}$$

and

$$\sigma_b^2 = \frac{\sigma^2 \sum \frac{1}{V_i}}{\sum \frac{1}{V_i} \sum \frac{x_i^2}{V_i} - \left(\sum \frac{x_i}{V_i}\right)^2},$$

where all sums are taken from $i = 1, \ldots, n$. These expressions follow directly from standard equations for weighted regressions (Draper and Smith 1981). Then we may estimate power for arbitrary x_i and V_i as

$$1 - \beta = \Phi\left(z_\alpha - \frac{b}{\sigma_b}\right)$$

for a decreasing trend ($b < 0$), as

$$1 - \beta = \Phi\left(\frac{b}{\sigma_b} - z_{1-\alpha}\right)$$

for an increasing trend ($b > 0$), and as

$$1 - \beta = \Phi\left(z_{\alpha/2} - \frac{b}{\sigma_b}\right) + \Phi\left(\frac{b}{\sigma_b} - z_{1-\alpha/2}\right)$$

for a trend in either direction. If, as before, we assume that the variance at each point is V_i, we may take $\sigma^2 = 1$ (i.e., it is not estimated), and let Φ be the distribution function for the standard normal distribution. If the V_i are treated as weighting factors, we estimate the common error variance σ^2 from the residuals about the regression, replace z_α by $t_{\alpha,\mathrm{df}}$, and let Φ be the distribution function for the noncentral t distribution.

Finally, to test for simple patterns in the A_i, we may dispense with regression entirely and use the method of linear contrasts, as in ANOVA. Given independent estimates of abundance $\hat{A}_i$, $i = 1, \ldots, n$, with associated variances $\hat{V}_i$, we can test for a linear trend by choosing contrast coefficients c_i proportional to $x_i - \bar{x}$, computing

$$Z = \frac{\sum c_i \hat{A}_i}{(\sum c_i^2 \hat{V}_i)^{1/2}},$$

and comparing Z to a standard normal distribution. Again, this procedure implicitly assumes that the $\hat{V}_i$ have been estimated with "large" df: with different assumptions the test could be based on the t distribution. Power for this test is computed in a manner similar to the above, e.g., as

$$1 - \beta = \Phi\left[\frac{\sum c_i A_i}{(\sum c_i^2 V_i)^{1/2}} - z_{1-\alpha}\right]$$

for a one-sided test for an increasing trend, where A_i and V_i are generated by the alternative hypothesis for which power is being computed. Calculations of power by this method are identical to the results in Gerrodette (1987), except for slight differences in some cases resulting from using the variances V_i directly rather than using the mean variance as an approximation (see Appendix). However, the contrast method is considerably more flexible: it allows the x_i to be unequally spaced (for example, if surveys were not conducted at equal intervals), it allows the V_i to follow any pattern (for example, if sampling effort or survey methods changed), and it allows other, nonlinear patterns in the A_i to be tested by choosing other coefficients c_i, subject to the condition that $\sum c_i = 0$.

Reporting of statistical power is widely neglected in ecological work (Peterman 1990). Although not a difficult concept, power is unfamiliar to many ecologists, and its calculation and use are easily misunderstood. For example, Link and Hatfield (1990) correctly point out that the formula for the confidence interval and standard error given on p. 1368 of Gerrodette (1987) is in error. The formula should apply to b, the estimated slope of the regression line, not r, the rate of change, and I would add that the formula is out of place in any case because it does not directly refer to power. However, Link and Hatfield go on to provide methods for estimating *r*. Their procedure gives an estimate of *r* for a particular set of data, but the answer is irrelevant for a power analysis. This is most easily seen by noting that the equations they give for *r* do not involve either α or β, the probabilities of statistical error of main interest in a power analysis. Link and Hatfield have answered the question: "What is the best estimate of *r*, given the data at hand?" However, the question of interest for a power analysis is: "What is the minimum *r* that will give a significant result, with controlled Type 1 and 2 errors, if the experiment were to be carried out under the stated conditions?"

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Literature Cited

Cohen, J. 1988. Statistical power analysis for the behavioral sciences. Lawrence Erlbaum, Hillsdale, New Jersey, USA.

Draper, N. R., and H. Smith. 1981. Applied regression analysis. John Wiley & Sons, New York, New York, USA.

Gerrodette, T. 1987. A power analysis for detecting trends. Ecology **68**:1364–1372.

Goldstein, R. 1989. Power and sample size via MS/PC-DOS computers. American Statistician **43**:253–260.

Link, W. A., and J. S. Hatfield. 1990. Power calculations and model selection for trend analysis: a comment. Ecology **71**:1217–1220.

Owen, D. B. 1965. The power of Student's *t*-test. Journal of the American Statistical Association **60**:320–333.

Park, H. 1972. Tables of percentage points of the non-central t-distribution. Technical Report Number 152, Department of Operations Research and Department of Statistics, Stanford University, Stanford, California, USA.

Peterman, R. M. 1990. The importance of reporting statistical power: the forest decline and acidic deposition example. Ecology **71**:2024–2027.

Resnikoff, G. J., and G. J. Lieberman. 1957. Tables of the non-central *t*-distribution. Stanford University Press, Stanford, California, USA.

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APPENDIX

Under the models proposed by Gerrodette (1987), Link and Hatfield (1990, Appendix) gave an exact expression for the error variance σ^2 (which they labelled $\sigma_b{}^2$) as

$$\sigma^2 = \frac{3(n+1)^2 \Sigma V_i - 12(n+1) \Sigma i V_i + 12 \Sigma i^2 V_i}{n(n+1)(n-1)},$$

where all sums are taken from 1 to *n*. Gerrodette (1987) approximated the same quantity (which he labelled $\sigma_{res}{}^2$) as the simple arithmetic average of the variances $\Sigma V_i/n$. Link and Hatfield's expression can be written as

$$\sigma^2 = \frac{\Sigma i^2 V_i - (n+1) \Sigma i V_i + \left(\frac{n+1}{2}\right)^2 \Sigma V_i}{n \frac{(n+1)(n-1)}{12}}$$

$$= \frac{\Sigma V_i (i - \bar{i})^2}{\Sigma (i - \bar{i})^2}.$$

This is an average of the V_i weighted by the squared deviations of the *i*'s from their mean. Because of the symmetrical nature of the series $(i - \bar{i})^2$, $i = 1, \ldots, n$, and the regular pattern of V_i ($V_i \propto A_i{}^q$, $q = 1, 2, 3$), the arithmetic mean will equal the weighted mean for $q = 1$ with the linear model and for $q = 2$ with the exponential model, and will differ only slightly for other combinations of *q* and model with *n* in the small-to-moderate range under consideration.

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Monitoring Trends in Dolphin Abundance in the Eastern Tropical Pacific: Analysis of 1989 Data

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ABSTRACT

Between July and December, 1989, the National Marine Fisheries Service conducted the fourth in its series of long-term research vessel surveys to estimate the relative abundance of dolphin populations in the eastern tropical Pacific Ocean. The five species of primary interest for these surveys, spotted, spinner, striped, common and Fraser's dolphins, are taken incidentally by tuna purse seiners. The relative abundance of sixteen stocks of these five species were estimated using line transect surveys from two ships operating for approximately 120 days each. Estimates of relative abundance for all stocks of spotted, spinner and Fraser's dolphins were substantially higher than 1988 estimates. Estimates of relative abundance for all stocks of common and striped dolphins were lower than 1988, but higher than 1986 or 1987.

INTRODUCTION

The National Marine Fisheries Service (NMFS) is responsible for assessing the status of dolphin stocks taken incidentally by tuna purse seiners in the eastern tropical Pacific (ETP). The major populations affected by the fishery are the northern offshore stock of spotted dolphins, *Stenella attenuata* and eastern and whitebelly stocks of spinner dolphins, *S. longirostris* (Smith, 1983). Common dolphins, *Delphinus delphis*, striped dolphins, *S. coeruleoalba* and Fraser's dolphins, *Lagenodelphis hosei* are also taken. These five species are grouped together and termed target species.

In 1986, the NMFS initiated a long-term (six year) research program to monitor relative abundance of dolphin populations in the ETP. The program utilizes two research vessels annually for 120 days each. The research design for the surveys indicated that a 10% annual rate of decrease in northern offshore spotted dolphins could be detected (a total 41% decrease over six surveys) with alpha and beta error levels of 10% (Holt *et al.*, 1987). Annual surveys were carried out in 1986, 1987, and 1988, and the results have been published (Holt and Sexton, 1989; 1990a; b; Sexton *et al.*, 1991). In 1989, the NMFS conducted the fourth survey utilizing the same vessels during the same times of the year. Here we present relative abundance estimates for the 1989 data and briefly compare these results to earlier values. Analyses of overall trends in population sizes will be carried out after the series of six surveys is complete in 1991.

MATERIALS AND METHODS

Study area and survey coverage

The same stratified study area was surveyed as in 1986 (Holt and Sexton, 1990b). The NOAA research vessels *David Starr Jordan* and *McArthur* traversed predetermined tracklines in the ETP from 29 July through 7 December (Fig. 1). Each ship was scheduled to spend approximately 120 days at sea, surveying tracklines similar to the previous three years. Due to logistical problems, however, the *Jordan* had to make several unscheduled port stops. Both ships also had to be diverted from scheduled port calls in Panama due to unsettled political conditions. Detailed data collection procedures and data summaries for each ship are presented by Hill *et al.* (1990a; b).

Each vessel had two teams of three observers each. The teams alternated watch every two hours. While on duty, two observers from the team used 25X binoculars to search from directly ahead to abeam of their respective sides of the ship. The third observer served as data recorder and searched directly ahead of the ship when not recording data. Each member of the team spent approximately equal time at each of these duty stations. Observers switched vessels at the mid-point of the cruises.

When possible, schools were approached and observers recorded independent 'best' estimates of school size. In some cases, an observer obtained a 'minimum' estimate but could not provide a best estimate. Estimates were averaged to obtain mean minimum and best estimates. When weather conditions were suitable, a Hughes 500D helicopter, based aboard the *Jordan*, was used to photograph schools whose sizes were estimated by the observers. The photographs will be used to calibrate observer estimates of school sizes.

Relative abundance estimation

Methods of estimating relative abundance of ETP dolphin populations followed Sexton *et al.* (1991) in order to provide comparable numbers. Estimates of relative population abundance (N_{ij}) of stock j, species i were computed as

$$N_{ij} = (D\ S\ P_t\ P_i\ A)\ ((A_{ij} + P'_{ij}\ A'_{ij}) / A_i), \qquad (1)$$

where

D = density of schools of all dolphin species over total study area,

S = mean size of schools of all target species,

P_t = proportion of all dolphin schools which are target schools,

P_i = proportion of individuals of species i in target schools,

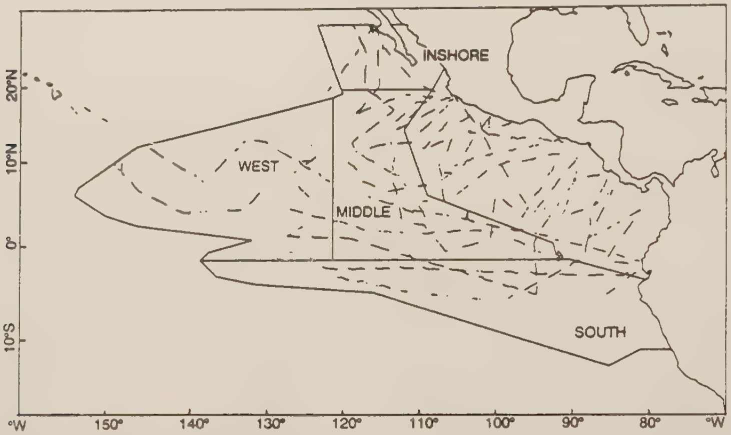

Fig. 1. Tracklines traversed while on searching effort by the NOAA R/V *David Starr Jordan* and *McArthur* during the 1989 survey.

P'_{ij} = proportion of individuals of stock j of species i in target schools in overlap region containing two stocks of species i (overlap region discussed below),

A = total area inhabited by all target species,

A_i = area inhabited by species i,

A_{ij} = area inhabited by species i, stock j, not overlapping with any other stock of species i, and

A'_{ij} = area inhabited by species i, stock j, in overlap region (discussed below).

This is the same method of estimation of abundance as in previous years, although the notation of equation (1) is somewhat different from that of Holt and Sexton (1990a; b). The summation has been eliminated because pooled estimates of D, S, P_t, and P_i have been used (Sexton *et al.*, 1991). Values for A_i, A'_{ij}, and A_{ij} are given in Holt and Sexton (1990b). Estimates of D, S, P_t, and P_i are based on sightings made while on searching effort within the study area in sea state conditions of Beaufort 5 or less.

The variance of N_{ij} was calculated using bootstrap methods (Efron, 1982). Over the entire study area, the number of legs of searching effort was tabulated and then an equal number of legs was randomly selected with replacement. This effort and the associated sightings were used to calculate D, P_t, S, P_i and, finally, estimates of N_{ij}s. This process was repeated 100 times. The variance of N_{ij} for each stock was calculated using these 100 estimates.

Formulae used to estimate school density are from Burnham *et al.* (1980), Holt (1985; 1987) and Hayes and Buckland (1983). The hazard rate model (Hayes and Buckland, 1983; Buckland, 1985) provided adequate fits (chi-square test) to the data and was used in the 1986, 1987 and 1988 analyses. Because of small sample sizes, *f(0)*, the sighting probability density function evaluated at the trackline, was calculated for data pooled over all strata and used to calculate density for the entire study area. Of schools containing both target and non-target species, only the proportion of individuals of the target species was used in estimating S. Estimates of the P_t were calculated using formulae presented by Holt and Powers (1982). Formulae to estimate P_i are given by Barlow and Holt (1986).

All species of dolphins encountered in the study area were included in the density analyses. Estimates of density, school size and species proportions were calculated using only schools containing 15 or more animals. Smaller schools were not used because they are difficult to detect, especially during rough weather (Holt, 1987). Similarly, because there is a direct correlation between the size of a school and the probability of it being detected (Drummer and McDonald, 1987), schools detected at increasing distances from the trackline tend to include disproportionately more large schools. This biases school size estimates upward and species proportions toward species which occur in large schools. However, the bias may be constant from year to year and hence not a serious source of error for detecting trends. Finally, schools for which there were no 'best' estimates were not used in the school size or species proportion calculations, but were used in the school density estimates if the 'minimum' estimate was 15 or more animals.

Only schools detected within 3.7 km (2.0 n.miles) perpendicular distance of the trackline were used for calculating components. A 3.7-km truncation point provided an adequate fit of the hazard model to the perpendicular distance distribution data while minimizing bias due to sighting larger schools at greater distances. Schools detected at distances greater than 3.7 km had little effect on the density estimates (Sexton *et al.*, 1991).

The outside boundary of the study area (Fig. 1) was described by Au *et al.* (1979) while the boundaries for each stock within the study area were described by Perrin *et al.* (1984). The study area was partitioned into four strata. The size of each stratum and the area occupied by each stock in each stratum were calculated by Holt and Sexton (1990b).

Most stocks are defined by geographic area, but some stocks of the same species overlap geographic areas. The last factor in Equation (1) contains terms to adjust for the overlap areas (A'_{ij}s). The overlapping stocks include (1) coastal and northern spotted, (2) eastern and whitebelly spinner and (3) Baja neritic and northern common dolphins (Perrin *et al.*, 1984). However, few data were available to determine relative proportions of the overlapping Baja neritic and northern common dolphins. Therefore, population estimates for these were combined. For overlapping stocks of spotted and spinner dolphins, the relative proportions of coastal and northern offshore spotted and of eastern and whitebelly spinner stocks within their area of overlap (P'_{ij}) were calculated as the bootstrap averages of their percent occurrence. As with the other estimates, data were pooled over strata within the region of overlap when calculating the bootstrap estimates.

RESULTS

During the 1989 survey, observers aboard both vessels searched 27,464 km and made 1,245 marine mammal sightings (Hill *et al.*, 1990a; b). In the study area (Fig. 1) and during Beaufort sea states of 5 or less, observers searched 26,846 km and detected 350 dolphin schools within 3.7 km of the trackline and for which a best or minimum estimate of school size was 15 or more (Table 1). Searching effort varied among strata according to the study design; for example, the inshore stratum had 30% of the area, 41% of the searching effort in 1989, and 52% (182/350) of all dolphin schools sighted. The estimate of $f(0)$ was 0.6025 for the whole study area.

Estimates of dolphin school density and species proportions are also presented in Table 1. Estimates of D calculated using the pooled $f(0)$ value above ranged from 2.25 to 4.99 schools/1000 km^2 among the different strata, with an estimate for the total area of 3.93. Estimates of S ranged from 139 to 240, with a total mean estimate of 165.0. The proportion of identified dolphin schools that included target species ranged from 0.776 to 0.931, with a total mean estimate of 0.872. The species proportions of target dolphin schools varied among strata. In the inshore and middle areas, for example, 36% of the target dolphins were spotted dolphins, while in the southern stratum, common (46%) and striped (35%) predominated. The estimated proportions of animals in each of the five target species for the whole study area were 0.332, 0.222, 0.239, 0.172, and 0.035 for spotted, spinner, common, striped and Fraser's dolphins, respectively.

Data on species proportions in the regions of stock overlap are presented in the lower part of Table 1. Only six spotted dolphin schools were seen in the overlap region of the coastal and offshore spotted stocks, and five of these were of the offshore stock. In the overlap area of eastern and whitebelly spinner stocks, 85 schools were seen of which 64 were eastern spinner schools.

Estimates of relative abundance in 1989 for each target species based on Equation 1 are presented in Table 2. The indices of relative abundance are calculated using the pooled estimates of D, S, P_t and P_i given in the right hand column of Table 1. Estimates of relative abundance for each stock of each species are also presented in Table 2. Note, as explained above, that these stock estimates are derived from the species estimates, with the stock estimates proportional to the areas the stocks are thought to occupy as described in Perrin *et al.* (1984), with adjustments made in the two cases (eastern/whitebelly spinner, coastal/northern offshore spotted) of stocks that overlap geographically. The relative abundance of spotted dolphins in the study area is estimated at nearly 3,600,000, with 79% being northern offshore spotted dolphins. The relative abundance of spinner dolphins is approximately 2,400,000, half from the eastern spinner stock. Relative indices of common dolphins are estimated at 2,600,000, striped dolphins at 1,900,000 and Fraser's dolphins at 376,000.

DISCUSSION

The research vessel surveys reported here have carefully replicated previous surveys, using the same vessels, the same area, the same time of year, the same sighting and recording methods, and most of the same observers. While questions remain about whether all assumptions of line transect theory have been satisfied, and thus whether the estimates of abundance can be considered absolute, the surveys were designed to detect trends in relative abundance (Holt, 1987). The analysis of the data has concentrated on producing a consistent index of abundance; for this reason, dolphin schools fewer than 15 in number and more than 3.7 km (2.0 n.miles) distant from the trackline have not been included in the analysis (Holt

Table 1

Summary of 1989 dolphin survey in eastern tropical Pacific. Symbols corresponding to equation 1 are in parentheses after description. Abundance estimates in Table 2 are derived from Total column only.

	Inshore	Middle	West	South	Total
Study area (1000 km^2) (A)	5,693	3,798	5,298	4,359	19,148
Percent of total study area	30	20	28	22	100
Trackline searched (km)	10,986	7,475	3,613	4,772	26,846
Percent of searching effort	41	28	13	18	100
School density (schools/1000km^2)(D)	4.99	3.67	2.25	3.16	3.93
Number dolphin schools detected	182	91	27	50	350
Mean target species school size (S)	139.11	170.79	240.48	205.03	165.04
Proportion target schools (P_t)	0.860	0.931	0.926	0.776	0.872
Proportion of dolphins within target school (P_i)					
Spotted	0.362	0.364	0.401	0.131	0.332
Spinner	0.236	0.204	0.417	0.049	0.222
Common	0.248	0.216	0.000	0.462	0.239
Striped	0.153	0.145	0.087	0.345	0.172
Fraser's	0.000	0.071	0.095	0.012	0.035
Stock proportions in overlap areas (P'_{ij})					
Coastal Spotted					0.042
Offshore Spotted					0.958
Number of schools in calculation					6
Eastern Spinner					0.707
Whitebelly Spinner					0.293
Number of schools in calculation					85

Table 2

Estimates of population size N_{ij} (in thousands of animals), standard error SE(N_{ij}), and coefficient of variation CV(N_{ij}) by stock and by species for all target dolphin species in the total study area of the eastern tropical Pacific. Stock estimates are proportional to the area occupied by each stock as determined in Perrin *et al.*, (1984), with additional adjustments made for the overlap between offshore and coastal spotted and between eastern and whitebelly spinner dolphins.

Dolphin Species and Stock	N_{ij}	SE(N_{ij})	CV(N_{ij})
Spotted *(Stenella attenuata)* total	3596.0	640.9	0.178
Coastal	36.3	6.5	0.178
Northern Offshore	2838.3	505.8	0.178
Southern Offshore	721.4	128.6	0.178
Spinner *(Stenella longirostris)* total	2,405.3	509.1	0.212
Costa Rican	35.1	7.	0.212
Eastern	1200.1	254.0	0.212
Northern Whitebelly	713.9	151.1	0.212
Southern Whitebelly	456.2	96.6	0.212
Common *(Delphinus delphis)* total	2,585.7	586.7	0.227
Northern tropical	411.2	93.3	0.227
West central tropical	735.9	167.0	0.227
East central tropical	825.1	187.2	0.227
Southern tropical	613.5	139.2	0.227
Striped *(Stenella coeruleoalba)* total	1855.9	286.3	0.154
Northern tropical	210.5	32.5	0.154
West central tropical	338.4	52.2	0.154
East central tropical	543.9	83.9	0.154
South tropical	763.1	117.7	0.154
Fraser's *(Lagenodelphis hosei)* total	375.8	172.7	0.460
Total of all target species	10,818.7	2,195.7	0.203

and Sexton, 1989; 1990a; b). The results for dolphin stocks reported here, therefore, should be considered relative indices of abundance to be compared to previous years, not estimates of absolute numbers of dolphins.

Results of the 1986, 1987 and 1988 surveys have been reported by Holt and Sexton (1989; 1990a; b). However, the methods of analysis varied slightly among these reports and the numbers are not strictly comparable, either with each other or with this report. Sexton *et al.* (1991) compared various methods of analysis, and concluded that an analysis using data pooled over all strata and species, with dolphins having an unweighted mean school size 15 or more at a distance not more than 3.7 km from the trackline, produced estimates of relative abundance with the smallest coefficient of variation. Sexton *et al.* (1991) reanalyzed the 1986–1988 data using these criteria to produce a set of comparable indices of abundance. The present report analyzes the data in the same way, and the results can thus be compared.

The estimate of relative abundance for each stock of spotted dolphins was considerably higher in 1989 than in 1988. The total estimate for all stocks of spotted dolphins increased 41% to nearly 3,600,000. Similarly, the estimate of relative abundance for each stock of spinner dolphins was substantially higher than in 1988. The total estimate for all stocks of spinner dolphins increased 38% to 2,400,000. The estimate of relative abundance for Fraser's dolphins increased from 110,800 to 375,800 between 1988 and 1989. Few of these dolphins were seen, however, and the standard errors of both the 1988 and 1989 estimates are large (Table 2). Increases of 41% and 38% for the more abundant spotted and spinner dolphins are clearly not possible in one year based on reproduction alone (Reilly and Barlow, 1986); such large changes between successive years may be due to immigration into the study area or estimation error; if so, this implies that the actual precision of the estimates is underestimated. These possible explanations for the increases seen between 1988 and 1989 (recruitment, immigration, and estimation error) are not mutually exclusive, and some combination of them may explain the results.

The estimate of relative abundance for each stock of common dolphins was substantially lower in 1989 than in 1988. The total estimate for all stocks of common dolphins decreased 51% to 2,600,000. The 1986 and 1987 estimates, both total and for each stock of common dolphins, were also much lower than the 1988 estimates. The 1989 estimates are therefore more similar to the 1986 and 1987 than to the 1988 estimates, but remain higher than either of the former. Likewise, the estimate of relative abundance for each stock of striped dolphins was lower in 1989 than in 1988, but higher than in either 1986 or 1987. The estimate of relative abundance for all stocks of striped dolphins combined declined 18% to 1,900,000.

For all five target species combined, the estimate of relative abundance decreased from 11,900,000 in 1988 to 10,800,000 in 1989, an overall decrease of 9%. Such a decrease is not statistically significant based on the estimated standard error of approximately 2,200,000. The estimated coefficients of variation for each species are similar to previous years, ranging from 0.15 to 0.23 for all species except Fraser's dolphins, which are much higher (0.46).

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REFERENCES

Au, D., Perryman, W.L. and Perrin, W. 1979. Dolphin distribution and the relationship to environmental features in the eastern tropical Pacific. Southwest Fish. Cent. Adm. Rep. No. LJ-79-43. 59pp.

Barlow, J. and Holt, R.S. 1986. Proportions of species of dolphins in the eastern tropical Pacific. U.S. Dep. Commer., Report NOAA-TM-NMFS-SWFC-56. 44pp.

Buckland, S.T. 1985. Perpendicular distance models for line transect sampling. *Biometrics* 41:177–95.

Burnham, K.P., Anderson, D.R. and Laake, J.F. 1980. Estimation of density from line transect sampling of biological populations. *Wildl. Monogr.* 72:1–202.

Drummer, T.D. and McDonald, L.L. 1987. Size bias in line transect sampling. *Biometrics* 43:13–21.

Efron, B. 1982. The jackknife, the bootstrap, and other resampling methods. SIAM, monograph No.38, CBMS-NSF. 92pp.

Hayes, R.J. and Buckland, S.T. 1983. Radial distance models for the line transect method. *Biometrics* 39:29–42.

Hill, P.S., Jackson, A. and Gerrodette, T. 1990a. Report of a marine mammal survey of the eastern tropical Pacific aboard the research vessel *David Starr Jordan* July 29-December 7, 1989. U.S. Dep. Commer., NOAA-TM-NMFS-SWFC-142. 143pp.

Hill, P.S., Jackson, A. and Gerrodette, T. 1990b. Report of a marine mammal survey of the eastern tropical Pacific aboard the research vessel *McArthur* July 29-December 7, 1989. U.S. Dep. Commer., NOAA-TM-NMFS-SWFC-143. 132pp.

Holt, R.S. 1985. Estimates of abundance of dolphin stocks taken incidentally in the eastern tropical Pacific yellowfin tuna fishery. Southwest Fish. Cent. Adm. Rep. No. LJ-85-20. 32pp.

Holt, R.S. 1987. Estimating density of dolphin schools in the eastern tropical Pacific Ocean by line transect methods. *Fish. Bull., US* 85(3):419–34.

Holt, R.S. and Powers, J.E. 1982. Abundance estimation of dolphin stocks in the eastern tropical Pacific yellowfin tuna fishery determined from aerial and ship surveys to 1979. U.S. Dep. Commer., NOAA-TM-NMFS-SWFC-23, 95pp.

Holt, R.S. and Sexton, S.N. 1989. Monitoring trends in dolphin abundance in the eastern tropical Pacific using research vessels over a long sampling period: analyses of 1987 data. *Rep. int. Whal. Commn* 39:347–51.

Holt, R.S. and Sexton, S.N. 1990a. Monitoring trends in dolphin abundance in the eastern tropical Pacific using research vessels over a long sampling period: analyses of 1988 data. *Rep. int. Whal. Commn* 40:471–6.

Holt, R.S. and Sexton, S.N. 1990b. Monitoring trends in dolphin abundance in the eastern tropical Pacific using research vessels over a long sampling period: analyses of 1986 data, the first year. *Fish. Bull., US* 88(1):105–11.

Holt, R.S., Gerrodette, T. and Cologne, J.B. 1987. Research vessel survey design for monitoring dolphin abundance in the eastern tropical Pacific. *Fish. Bull., US* 85(3):435–46.

Perrin, W.F., Scott, M.D., Walker, G.J. and Cass, V.L. 1984. Review of geographical stocks of tropical dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern Pacific. Southwest Fish. Cent. Adm. Rep. No. LJ-87-02, 68pp.

Reilly, S.B. and Barlow, J. 1986. Rates of increase in dolphin population size. *Fish. Bull., US* 84(3):527–33.

Sexton, S.N., Holt, R.S. and DeMaster, D.P. 1991. Investigating parameters affecting relative estimates in dolphin abundance in the eastern tropical Pacific from research vessels in 1986, 1987 and 1988. Paper SC/42/SM43 (published in this volume).

Smith, T.D. 1983. Changes in size of three dolphin (*Stenella* spp.) populations in the eastern tropical Pacific. *Fish. Bull., US* 81:1–14.

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Changes in Catchability in a Bottom-Trawl Fishery for Cape Hake (*Merluccius capensis*)

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Management of the Cape hake (*Merluccius capensis*) stock off the coasts of Angola and Namibia has been based on surplus production modeling, which incorporates an assumption of constant catchability. Results of least-squares catch-at-age analysis and virtual population analysis were used to estimate catchability from 1968 to 1986. Estimated catchability was either relatively constant or gradually increasing from 1968 to 1978, but fluctuated considerably between about 1979 and 1983. The fluctuations may have been due to an inverse relationship between catchability and abundance or to environmental factors affecting fish distribution. The period of highest estimated catchability corresponded to the period of lowest estimated abundance and below-average water temperatures. If management is based on the assumption of constant catchability but catchability is inversely related to abundance, the risk of overfishing will be greatest when the stock is at the lowest levels. Future assessments should place increased reliance on survey data or incorporate an appropriate model of catchability changes.

La gestion du stock de merlu du Cap (*Merluccius capensis*) de la côte de l'Angola et de la Namibie s'est fondée sur la modélisation de la production excédentaire, avec un potentiel de capture supposé constant. Pour estimer le potentiel de capture, de 1968 à 1986, on s'est servi de l'analyse des prises par classes d'âge par la méthode des moindres carrés et de l'analyse de la population virtuelle. Le potentiel de capture estimatif a été, soit relativement constant, soit graduellement croissant, de 1968 à 1978, mais il a considérablement fluctué entre 1979 et 1983. Les fluctuations observées étaient peut-être dues à une relation inverse entre le potentiel de capture et l'abondance ou à l'influence de facteurs du milieu sur la distribution des poissons. La période où le potentiel de capture estimé était le plus élevé correspond à la période où la valeur estimative de l'abondance était la plus faible et les températures de l'eau, sous la moyenne. Lorsque la gestion se base sur un potentiel de capture supposé constant et que ce potentiel est une fonction inverse de l'abondance, le risque de surpêche est maximal lorsque le stock est au plus bas. À l'avenir dans les évaluations, il faudrait se fier davantage aux résultats des relevés ou utiliser le modèle approprié, avec variations de potentiel de capture.

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A substantial fishery for Cape hake (*Merluccius capensis*) has existed off the coasts of Angola and Namibia since 1965. Landings from latitude 15 to 25°S (statistical divisions 1.3 and 1.4 of the International Commission for the Southeast Atlantic Fisheries (ICSEAF)) ranged from 90 500 tonnes (t) in 1980 to 606 100 t in 1972 (Table 1). Catches are made primarily with bottom-trawl gear although some catches are made at night in a midwater-trawl fishery (Crawford et al. 1987) for species such as horse mackerel (*Trachurus* spp.).

Both a surplus production model (Graham 1935) and virtual population analysis (VPA) (Murphy 1965) have been used to assess the status of the hake stock. Effort data used in the surplus production models were obtained from average weighted catch-per-unit-effort (CPUE) data, specifically tonnes per hour fished by Spanish bottom trawlers in tonnage class 7 (1000–1999 GRT). This weighted CPUE index, based on total catch and effort by fleet, is equivalent to using power factors to adjust for differences in catch rate (Andrew 1986).

A potential limitation of the surplus production model used to manage the hake fishery is the assumption that catchability (q) is constant. That assumption is used to relate observed fishing effort in year y ($f(y)$) to fishing mortality ($F(y)$):

$$F(y) = qf(y).$$

Based on that assumption, CPUE and abundance should be linearly related and management could be based on the CPUE data alone. The assumption that catchability is constant has been shown to be invalid for a number of pelagic species (Abramson and Tomlinson 1972; Fox 1974; MacCall 1976; Peterman and Steer 1981; Shelton and Armstrong 1983; Winters and Wheeler 1985) because of the interaction between fishermen and schooling fishes. Search time is an important component of total effort in many pelagic fisheries whereas the catch per unit of fishing time may simply reflect the within-school density (Paloheimo and Dickie 1964). If within-school density is maintained as abundance decreases, there would be an inverse relationship

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TABLE 1. Catch (thousands of tonnes) and standardized fishing effort (estimated hours fished in ICSEAF divisions 1.3 and 1.4 by Spanish bottom trawlers in tonnage class 7 (1000–1999 GRT)) (Draganik and Sacks 1987).

Year	Catch	Effort
1965	93.5	52 500
1966	212.4	162 500
1967	195.0	214 000
1968	382.7	399 000
1969	320.5	364 000
1970	402.5	447 000
1971	365.6	420 000
1972	606.1	842 000
1973	377.6	662 456
1974	318.8	708 400
1975	309.4	737 000
1976	369.8	880 476
1977	277.5	566 300
1978	258.1	600 200
1979	172.3	430 700
1980	90.5	201 100
1981	92.1	167 500
1982	176.4	332 800
1983	215.8	372 100
1984	228.5	357 000
1985	211.5	320 450
1986	230.9	355 230

between abundance and catchability. An inverse relationship also has been detected for several demersal species (Pope and Garrod 1975; Houghton and Flatman 1980; Angelsen and Olsen 1987; Crecco and Overholtz 1990), and it has been suggested that depensatory fishing mortality at low abundance levels is a general phenomenon among most commercial fisheries (Winters and Wheeler 1985; Crecco and Overholtz 1990).

Radovich (1982) noted that catchability will be constant only if (1) fishes are uniformly distributed over the fishing area, (2) effort is distributed randomly over the fishing area, and (3) units of effort are independent. The first assumption is unlikely to be true for Cape hake because schooling behavior has been observed for fish younger than age 2, and older fish form aggregations and migrate to spawning grounds (Shannon and Pillar 1986). The latter two assumptions are almost certainly violated because fishermen work cooperatively to locate and exploit areas of good catches. A preliminary analysis of catch-at-age data from ICSEAF division 1.5 provides evidence that catchability may be an inverse function of biomass (Gordoa and Pertierra 1987). The reliability of those results is unknown, however, because of a limitation in the catch data. Division 1.5 catches contain two hake species (*M. paradoxus* and *M. capensis*) that are quite similar in appearance; unfortunately, the proportion of the two species in historical commercial catches is not known.

The objective of this study was to examine the constant catchability assumption for the Cape hake fishery in divisions 1.3 and 1.4. We used results from VPA and least-squares analysis (Deriso et al. 1985) of the catch-at-age data to estimate fishing mortality rates and catchabilities. Observed trends in catchability were compared with estimates of abundance and information on environmental changes in order to develop hypotheses about the causes of changes in catchability.

Methods

Catch-at-age data for ages 1–10 were available for 1968–86 (Table 2). Catches of fish older than age 10 were negligible. The age composition estimates were obtained through an at-sea sampling program in which three to four observers measured about 100 000 fish and collected about 5000–6000 otoliths annually. The smallest hake require more time to process and are less valuable; consequently, catches of age 1 hake were underestimated prior to 1973 due to discarding. Discarding is believed to have been negligible in more recent years because of the relatively lower catches of older fishes.

Estimates of fishing mortality rates and catchability coefficients were based on results of VPA and least-squares catch-at-age analysis. The primary advantage of the VPA, which was done by Draganik and Sacks (1987), was that selectivity patterns could vary from year to year. The selectivity pattern for the least-squares analysis was assumed to be constant over selected ranges of years. Because of that simplifying assumption, an advantage of the least-squares analysis was that many fewer parameters had to be estimated. Another advantage was the assumption that catch and effort were measured with error; thus, residuals could be examined for evidence of lack of fit due to violations in the model assumptions (e.g. trends in the effort residuals due to changes in catchability).

The methods used by Draganik and Sacks (1987) in the VPA can be summarized as follows. A linear regression of the average F for ages 1–7 versus standardized fishing effort (from the weighted average CPUE index described above) was fitted using VPA results for 1968–82. The resulting regression equation was used to predict average F's for 1982–86. The selected starting F for the VPA was the value that minimized the squared difference between the 1982–86 average F's for ages 1–7 and the values predicted from the regression equation. (The starting F for age 10 fish was assumed to be constant over all years. The starting F's in 1986 for ages less than the assumed age at full recruitment (age 4) were based on an assumed selectivity pattern.) A natural mortality rate (M) of 0.3 was assumed for all ages and years.

The least-squares model that we used (Deriso et al. 1985) was based on the following assumptions: (1) fishing mortality could be separated into an age-dependent factor (selectivity) and a year-dependent factor (the fishing mortality rate for fully recruited fish, $F(y)$), (2) catchability was constant and predicted fishing effort ($f'(y)$) was obtained as $F(y)/q$, and (3) errors in measuring catch and fishing effort were lognormally distributed. The microcomputer program CAGEAN (Deriso et al. 1985) was used to estimate the model parameters. As in the VPA, we assumed that M was 0.3 for all ages and years (Draganik and Sacks 1987).

Several model parameters were varied to evaluate the model's sensitivity to assumptions about catchability and selectivity. We varied the weighting factor (λ) used to adjust the amount of influence given the auxiliary information on fishing effort (Table 1). A low λ value (1.0) permitted predicted and observed effort to deviate considerably whereas a larger value (10.0) forced relatively close agreement (and adherence to the constant catchability assumption). We were unable to obtain solutions for λ values greater than 10, suggesting an inconsistency between the catch-at-age and effort data.

We evaluated three alternative assumptions about the range of years for which a constant selectivity pattern was assumed to apply: (1) a single selectivity period from 1968 to 1986, (2) two selectivity periods during which trawl mesh size was 70–120 mm (1968–75), or a minimum of 110 mm (1976–86) (Andrew and Butterworth 1988) and (3) selectivity periods 1968–81 and 1982–86 corresponding to the periods before and

TABLE 2. Number of Cape hake caught (in millions) in ICSEAF divisions 1.3 and 1.4 (from Draganik and Sacks 1987).

	Age									
Year	1	2	3	4	5	6	7	8	9	10
1968	2.72	89.83	561.14	193.77	74.17	11.64	2.45	0.00	0.00	0.00
1969	0.00	52.98	231.41	212.35	59.27	17.16	8.33	2.50	1.33	0.00
1970	0.13	128.47	320.82	203.83	110.20	21.97	7.37	1.15	0.67	0.00
1971	0.03	24.84	161.14	264.95	72.17	21.73	11.41	3.64	2.08	0.50
1972	2.91	48.67	549.59	346.37	119.41	38.32	19.59	3.68	1.36	0.63
1973	27.78	53.23	383.21	290.85	48.42	10.52	5.42	6.60	1.25	0.91
1974	32.41	162.77	160.17	60.34	103.79	57.22	15.27	2.62	1.28	0.69
1975	26.78	126.94	362.41	114.99	32.96	18.88	13.88	6.74	3.61	1.89
1976	71.41	345.29	500.98	120.59	14.23	12.90	2.25	1.69	0.80	0.40
1977	51.58	94.33	225.85	181.45	28.39	9.80	7.14	4.65	1.24	1.35
1978	48.49	434.71	307.54	74.92	36.89	11.07	1.69	0.38	0.64	0.11
1979	18.77	113.85	121.15	66.95	23.25	12.85	5.47	3.97	1.62	1.75
1980	44.05	36.19	49.52	40.41	12.89	9.86	4.08	1.35	0.64	0.76
1981	25.15	45.83	45.38	34.39	25.90	11.23	2.24	1.67	0.26	0.06
1982	135.80	312.31	168.97	47.96	13.30	7.34	4.75	2.65	1.01	0.46
1983	872.13	739.33	97.18	42.68	11.61	5.21	2.10	0.80	0.32	0.20
1984	34.76	667.31	295.07	54.26	17.00	5.88	1.63	1.42	0.11	0.76
1985	56.49	127.01	230.17	129.24	31.79	5.45	1.25	0.74	0.15	0.01
1986	25.50	301.40	135.40	114.50	69.10	20.10	10.40	2.50	0.80	0.00

after the entry of the apparently strong 1981 and 1982 year classes (i.e. targeting on strong year classes). We also obtained some estimates under the assumption that a range of ages (e.g. 3–5 or 4–6) were equally vulnerable to fishing; the results were similar to those reported here.

We used results from VPA to determine whether there had been obvious changes in selectivity patterns over time. Because the starting F's would have greatest impact on estimates for the oldest age groups, we calculated VPA selectivity estimates (i.e. age-specific F's for each year scaled to a maximum of 1.0) using F's for ages 1–7 only.

By varying the assumptions used in the least-squares analysis, we obtained a wide range of estimated population levels and fishing mortality rates. These solutions appeared to be about equally consistent with the observed catch data; consequently, we rejected some solutions by using the following two alternative sources of recruitment estimates.

(1) Annual trawl survey estimates of absolute abundance have been obtained each August since 1983 using the swept-area method, based on 20 d of trawling with four to five tows per day at randomly selected sites (Macpherson et al. 1985). These surveys were conducted over latitudes 23–30°S, compared with 15–25°S for the commercial catch data. Because of the lack of overlap and difference in coastline length, we used the survey estimates only to rule out extreme solutions.

(2) Based on the convergence property of VPA, we felt that the VPA estimates of recruitment for the 1968–77 year classes should be relatively reliable. For those year classes, the estimated abundance at age 1 was based on a starting F at age 10. The cumulative F for ages 1–9 exceeded 3.5 for each year class, which should be more than sufficient to insure convergence. The VPA estimate of mean recruitment from 1968 to 1977 was 1.67 billion recruits using a starting F of either 0.65 or 0.75 (Draganik and Sacks 1987). Based on those results, we believe that a mean 1968–77 recruitment level substantially different from 1.67 billion is unlikely at the assumed level of natural mortality.

For the catch-at-age analyses, we estimated the approximate overall catchability in year y ($q(y)$) as

$$q(y) = C(y)/(f(y)B_{\text{exp}}(y))$$

where $C(y)$ was the catch biomass and $B_{\text{exp}}(y)$ was the estimated exploitable biomass in year y. For VPA, we used the estimated selectivity patterns for ages 1–7 (described above) to determine exploitable biomass. Thus, our VPA estimate of catchability applied to ages 1–7 only. Crecco and Overholtz (1990) estimated catchability using total biomass; however, we used exploitable biomass in an attempt to separate selectivity and catchability changes.

Although constant catchability is assumed in the CAGEAN program, estimated catchability will vary among years due to differences between observed and predicted effort unless λ is large. Crecco and Overholtz (1990) used survey estimates of abundance and VPA estimates of catchability to test for a nonlinear relationship between abundance and catchability. In our study, both abundance and catchability were estimated using the catch-at-age data; consequently, no significance tests were carried out.

We examined the 23–30°S survey data for evidence of recent (1983–89) changes in the area occupied by *M. capensis*. For each year, we plotted cumulative distributions showing the proportion of total biomass from each survey stratum. A contraction in the area occupied by the stock would cause a larger proportion of the stock to occur in fewer strata.

Results

Estimated Abundance and Selectivity

The least-squares recruitment estimates were most consistent with the survey and VPA estimates and least sensitive to λ for the case where selectivity was assumed to have changed during 1982–86 (relative to 1968–81) in order to target on the apparently strong 1981 and 1982 year classes (Table 3). We estimated that fish ages 1–2 had increased vulnerability to

TABLE 3. Recruitment (billions of age 1 fish) as estimated by VPA (Draganik and Sacks 1987), the swept-area method using trawl survey catches (Macpherson and Roel 1984), and three least-squares analyses using different assumptions about selectivity. λ represents the relative weight given the auxiliary information on fishing effort in the least-squares analyses.

			Selectivity period					
			1968–86		1968–75, 1976–86		1968–81, 1982–86	
Year	VPA	Survey	λ = 1	λ = 10	λ = 1	λ = 10	λ = 1	λ = 10
1968	2.23		2.77	49.43	2.60	25.54	2.85	1.54
1969	2.10		1.21	21.02	1.19	10.54	1.25	0.79
1970	2.61		1.59	26.65	1.85	13.99	1.65	1.24
1971	1.33		0.93	15.68	1.15	8.36	0.94	0.78
1972	0.90		1.08	17.91	1.45	10.23	1.12	0.97
1973	1.60		2.21	36.05	2.86	21.74	2.30	2.11
1974	2.04		2.71	45.05	2.69	26.94	2.73	2.39
1975	1.45		2.53	42.41	2.49	22.39	2.49	2.01
1976	1.20		1.52	25.87	1.06	8.81	1.57	1.18
1977	1.26		1.63	29.21	0.99	9.40	1.77	1.09
1978	0.55		1.46	32.40	0.89	9.75	1.11	0.72
1979	0.44		1.15	29.58	0.65	8.14	0.63	0.52
1980	0.84		2.27	56.00	1.21	14.83	1.18	1.15
1981	1.20		3.37	80.79	1.73	19.45	2.10	1.84
1982	2.82		9.15	213.11	4.24	45.75	3.82	2.64
1983	3.18	3.75	17.74	376.05	6.69	64,70	5.86	3.49
1984	0.84	5.53	5.90	111.52	1.65	13.58	1.23	0.69
1985	1.42	5.38	21.29	343.04	3.48	25.79	2.25	1.21
1986	0.51	4.68	12.82	202.11	0.97	7.34	0.66	0.33
1987		2.51						
1988		1.46						
1989		2.21						

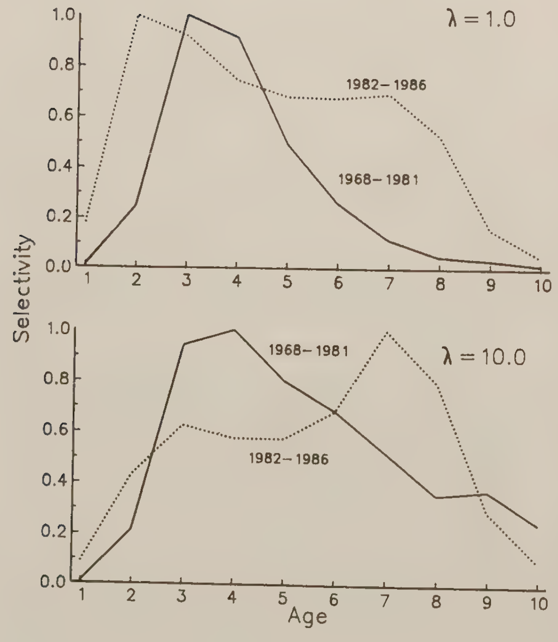

FIG. 1. Least-squares estimates of the selectivity patterns for periods 1968–81 and 1982–86. λ represents the relative weight given the auxiliary information on fishing effort.

fishing during 1982–86 relative to 1968–81 (Fig. 1); thus, the large recent catches were attributed both to strong recruitment and selectivity changes. The increased vulnerability of fish ages 1–2 also was evident in the 1982–85 selectivity patterns based on the VPA results (Fig. 2). There were no apparent trends in the least-squares catch residuals for this case, except that the predicted catches of age 1 fish were much larger than the observed catches during 1969–71 (i.e. years in which discarding was thought to occur.

When a single selectivity period (1968–86) was assumed, the large catches during 1982–86 were attributed solely to strong incoming year classes. The estimates of 1982–86 recruitment were considerably higher than either the survey or VPA estimates (Table 3). When selectivity periods 1968–75 and 1976–86 were assumed (before and after the minimum mesh regulation was implemented), recruitment estimates for λ = 1.0 were similar in magnitude to the survey and VPA estimates whereas the results for λ = 10.0 were substantially higher (Table 3). As in the previous case, recruitment estimates generally were highest during 1982–86. We did not find evidence in our VPA selectivity estimates (Fig. 2) of a consistent change in selectivity due to the minimum mesh regulation. Based on these results, we limit subsequent discussion of the least-squares analysis to the case where selectivity periods 1968–81 and 1982–86 were assumed.

The 1968 number-at-age vectors and resultant biomass estimates differed considerably for the two λ values (Fig. 3), although the biomass estimates converged somewhat by 1982 due to the similar estimates of recruitment during the 1970's (Fig. 4). The larger change in biomass from 1968 to 1982 corresponded to the larger change in predicted fishing effort, which was associated with the smaller λ value (Fig. 5). The

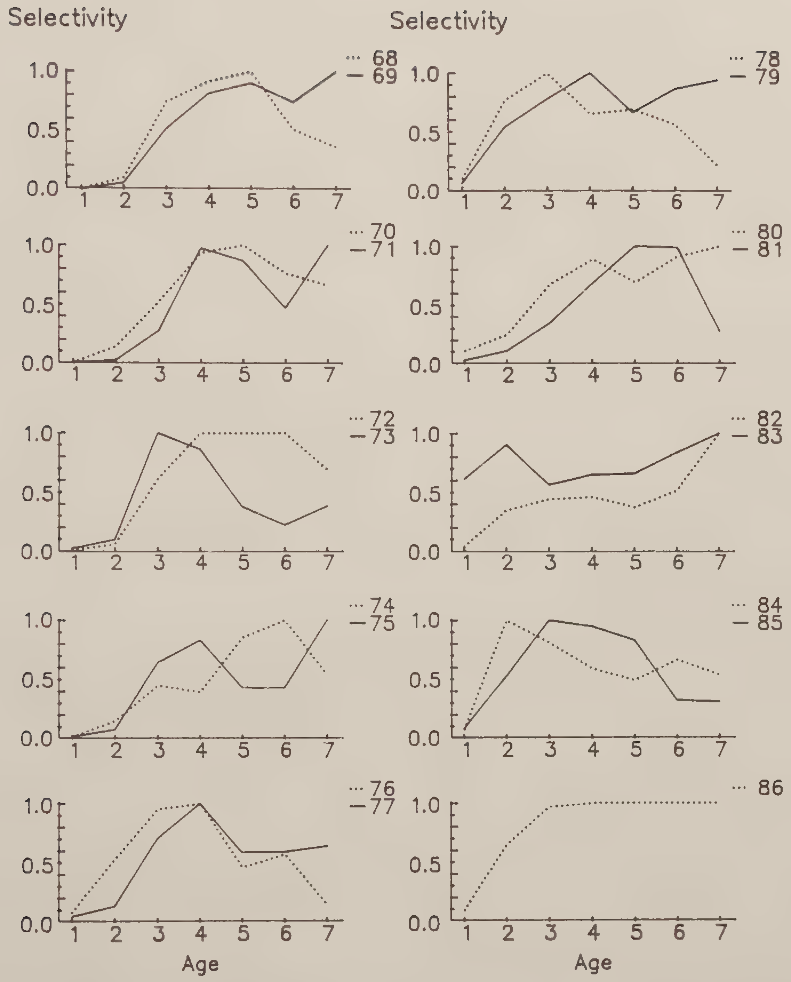

FIG. 2. Estimated annual selectivity patterns for fish ages 1–7, based on VPA results obtained by Draganik and Sacks (1987). Fishing mortality rates (F) for age 10 fish were assumed values. For that reason, F's for fish ages 8–10 were not used to calculate selectivities to reduce their impact on the estimated selectivity patterns.

change in biomass was much smaller when predicted and observed effort were forced to agree more closely.

Estimated Catchability Changes

The relative weight given the auxiliary information on fishing effort strongly affected the estimated F's, or equivalently, the predicted fishing effort levels (Fig. 5). When λ was low, predicted effort increased at a much faster rate from 1968 to 1979 than did observed effort. Observed and predicted effort levels were generally similar from 1983 to 1986.

Estimated catchability was relatively constant prior to about 1979 but fluctuated considerably between about 1979 and 1983 (Fig. 6). The decrease in catchability after 1981 corresponded to a period of increasing numerical abundance due to strong recent recruitment (Fig. 3). These changes resulted in an apparent inverse relationship between estimated abundance and catchability, particularly for the least-squares analysis with $\lambda = 1.0$ (Fig. 7). This relationship is highly tentative, however, because estimated total biomass appears as a variable on both axes of the catchability plot.

Changes in Spatial Distribution

The differences we observed in area occupied by *M. capensis* from 1983 to 1989 (Fig. 8) were not consistent with the changes in estimated biomass (Fig. 2). The apparent contraction in 1986 and 1987 did not persist in 1988 and 1989, despite further decreases in estimated biomass.

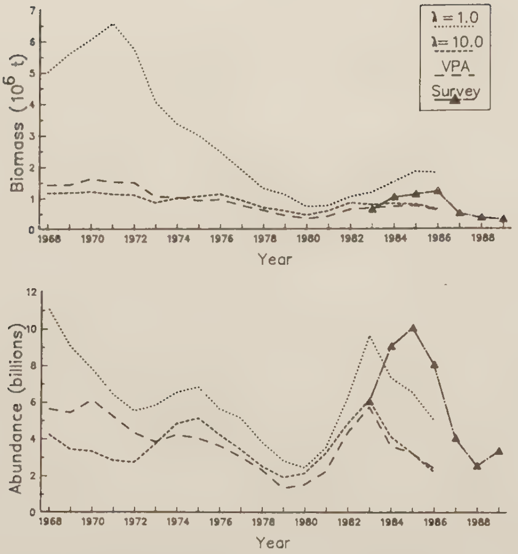

FIG. 3. Estimated levels of biomass and numerical abundance from 1968 to 1986, based on a least-squares catch-at-age analysis. λ represents the relative weight given the auxiliary information on fishing effort.

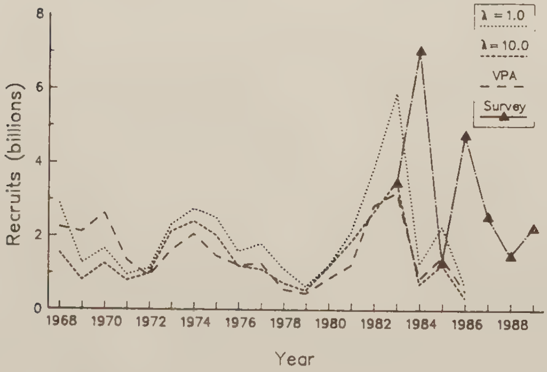

FIG. 4. Estimates of annual recruitment (billions of age 1 fish), based on a least-squares catch-at-age analysis (where λ represents the relative weight given the auxiliary information on fishing effort), VPA (Draganik and Sacks 1987), and swept-area estimates from 1983 to 1989 trawl surveys at latitudes 23–30°S (Macpherson and Roel 1984).

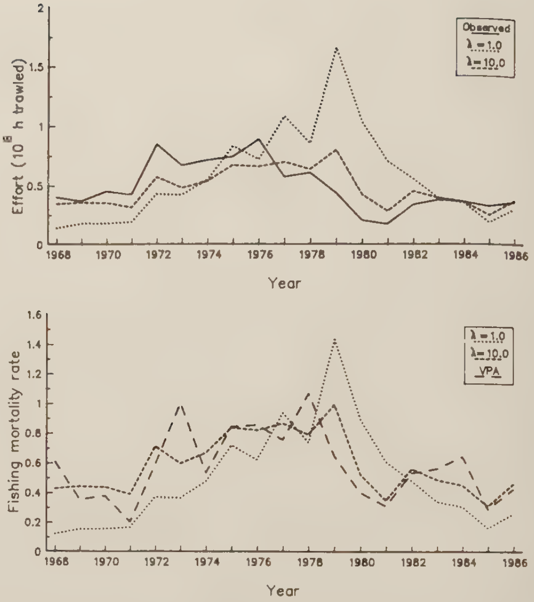

FIG. 5. Upper panel: observed fishing effort (Draganik and Sacks 1987) and predicted levels based on least-squares catch-at-age analysis. Lower panel: fishing mortality rates obtained from least-squares catch-at-age analysis and from VPA (Draganik and Sacks 1987). λ represents the relative weight given the auxiliary information on fishing effort in the catch-at-age analyses.

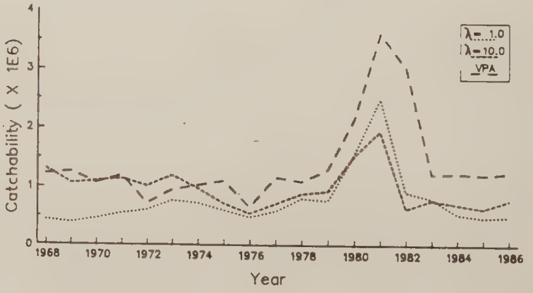

FIG. 6. Estimates of annual catchabilities obtained from least-squares catch-at-age analysis (where λ represents the relative weight given the auxiliary information on fishing effort) and from VPA (Draganik and Sacks 1987). Catchability estimates for VPA represent ages 1–7 only.

Discussion

Our recruitment estimates were highly sensitive to the assumption that the selectivity pattern was constant over time, and we obtained unreliable estimates for two of the three cases we examined. Our results supported earlier studies indicating that a model with more than one selectivity period was required (Butterworth et al. 1986a) and that the mesh regulation did not change overall catchability significantly (Andrew and Butterworth 1988). Butterworth et al. (1986a) examined the hypothesis that selectivity for young fish increased gradually from 1968 to 1983, due perhaps to changes in the spatial distribution of fishing effort. They concluded that the changes in catch-at-age data appeared more complex than could be accounted for by the selectivity submodel that they assumed. The results obtained in our study (based on three additional years of catch data) appear to support selectivity changes in response to fluctuations in year-class strength (i.e. targeting on strong year classes).

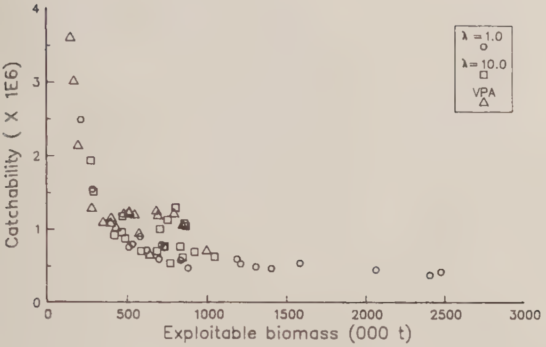

FIG. 7. Estimates of catchability versus exploitable biomass obtained from least-squares catch-at-age analysis (where λ represents the relative weight given the auxiliary information on fishing effort) and from VPA (Draganik and Sacks 1987). Catchability and exploitable biomass estimates for VPA represent ages 1–7 only.

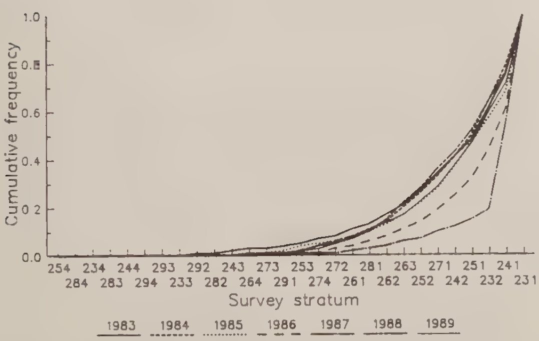

FIG. 8. Cumulative proportion of total biomass accounted for annually by each sampling stratum, based on trawl survey estimates of abundance for the area 23–30°S. Sampling strata are ordered from lowest to highest 1983–89 average catch rate.

The selectivity patterns from the least-squares analysis were sensitive to λ for 1982–86. Estimates for the latter selectivity period should stabilize over time as additional years of data are included in the analysis. For three of the four selectivity patterns, vulnerability to fishing decreased at older ages (Fig. 1). A similar trend was apparent in some of the VPA selectivity patterns, although those patterns varied substantially from year to year (Fig. 2). Decreased vulnerability for older fish may be reasonable because (1) vulnerability to trawl gear decreases at older ages for some species (e.g. Pacific whiting (*M. productus*), Hollowed et al. 1988; sablefish (*Anoplopoma fimbria*), Methot and Hightower 1988) and (2) Cape hake older than age 10 occur rarely in trawl catches but have been caught in exploratory fishing with hook-and-line gear.

An advantage of this and earlier catch-at-age analyses was the ability to identify alternative population trends that could account for the observed catch and effort patterns. In a traditional surplus production model, the recent increases in CPUE would be attributed to large increases in recruitment. In the catch-at-age analyses, the CPUE increases would be attributed either to strong recruitment or to moderate recruitment and changing selectivity and catchability. Because of discrepancies between results from surplus production and age-structured models, Butterworth et al. (1986a) hypothesized that the CPUE increases may have been due partly to a change in the spatial distribution of fishing effort. They suggested that the increased catches of young fish may have been due to increased fishing in inshore areas inhabited by younger hake. Our results suggest that the CPUE increases were due to a combination of changes in selectivity, catchability, and the strength of incoming year classes.

Estimated catchability generally increased from 1968 to 1981 in the catch-at-age analysis for the lower λ value (Fig. 6) because catchability changes could occur as a trend in the effort residuals. Those changes in estimated catchability would be consistent with increasing fishing power, due perhaps to increased knowledge of the fishing grounds or improvements in gear. For the least-squares analysis using the higher λ value, catchability was more constrained to fluctuate about a constant level.

If catchability increased gradually over time, then recent quotas derived from surplus production modeling would be overestimated (Butterworth and Andrew 1987). However, the fluctuations in catchability observed in all cases from about 1979 to 1983 suggested that factors other than changes in fishing power contributed to the observed trends. The temporal changes in estimated biomass and numerical abundance (Fig. 3) resulted in an apparent inverse relationship between estimated catchability and abundance (Fig. 7). Crecco and Overholtz (1990) noted a similar relationship for Georges Bank haddock (*Melanogrammus aeglefinus*), which they attributed to changes in the area occupied by the stock.

One explanation for an inverse relationship between catchability and abundance is that fish populations tend to contract toward the most favorable habitat as they are fished down (MacCall 1990). We did observe a substantial apparent contraction using the approach proposed by Crecco and Overholtz (1990) (for each year, summing the area of strata for which the catch rate exceeded the long-term median). However, based on the cumulative distribution plots (Fig. 8), we inferred that the decreases in stratum catch rates represented overall decreases in abundance. The apparent changes in spatial distribution for the area surveyed (23–30°S) (Fig. 8) were not consistent with changes in abundance in areas 1.3 and 1.4, but could be due to changes in other factors such as temperature or food availability. We are unable to determine whether the stock contracted during the period of highest estimated catchability because of the absence of survey data prior to 1983.

Changes in water temperature could have affected catchability. The period from 1979 to 1983 was one of below-average sea-surface temperatures (SST) for the Benguela system (McLain et al. 1985). Based on monthly mean SST for 3° blocks, anomalies of less than −0.5°C were observed during most of 1979–83, with greatest negative anomalies (less than −1°C) during November 1981 to May 1982 (McLain et al. 1985). Using SST data through 1984 in a modified catch-effort model, Butterworth (1988) reported a significant temperature effect on catchability assuming a 1-yr lag but none if a 0-yr lag was assumed.

If catchability is inversely related to abundance, management problems would be greatest when the stock declined to low levels: (1) biomass and catch quotas obtained from traditional surplus production models would tend to be overestimated (because catchability would be higher than the historical mean) and (2) further management errors would be likely when setting either effort or catch quotas because of the rapidly changing relationship between effort and fishing mortality (Gulland 1977; Winters and Wheeler 1985).

We agree with Butterworth (1988) that conservative management is warranted until the factors affecting catchability can be reliably determined. Our results suggest that catchability and selectivity have changed over time; however, the apparent changes in catchability would also bias our estimates of it. Less biased estimates of catchability (and abundance) could presumably be obtained by using survey estimates of abundance to constrain the catch-at-age analysis (Winters and Wheeler 1985; Butterworth 1988). In our study, survey abundance estimates from an overlapping area were compared with the results of catch-at-age analysis and VPA. The survey estimates were useful for rejecting highly implausible solutions, but temporal changes in survey abundance were at odds with the VPA and catch-at-age analysis results (Fig. 3 and 4). A precise survey of areas 1.3 and 1.4, preferably measuring absolute abundance (Kimura 1989), would eliminate the need for potentially biased estimates of fishing effort. An additional advantage of survey data would be the opportunity to test for a relationship between catchability and abundance (Crecco and Overholtz 1990).

An alternative approach for dealing with catchability changes over time would be to use both survey estimates of abundance and commercial fishing effort data, but to vary the weighting factors to determine the sensitivity of population trends to the two sources of auxiliary data. Another alternative, for either a surplus production or catch-at-age model, would be to define catchability as a function of stock size or age structure or a constant that differed among periods (Fox 1974; Butterworth et al. 1986b; Deriso et al. 1989). Given the difficulty of exactly modeling catchability changes over time, that approach might be more effective if survey data were available to help constrain the catch-at-age analysis. Other approaches include analyzing catch and effort data on a finer spatial scale to separate changes in abundance from changed fishing distribution patterns and conducting a detailed reexamination of vessel power factors used to combine effort among fleets (Butterworth 1988).

In summary, our results suggest that catchability has varied over time, due perhaps to changes in fishing power, resource abundance, or oceanographic factors. Improved estimates of abundance and short-term yield can be obtained by incorporating precise survey data or an appropriate submodel of catchability changes into either a surplus production or age-structured model. Conservative management is warranted until factors affecting catchability can be identified.

Acknowledgements

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References

Abramson, N. J., and P. K. Tomlinson. 1972. An application of yield models to a California shrimp population. U.S. Fish. Bull 70: 1021–1041.

Andrew, P. A. 1986. Dynamic catch-effort models for the southern African hake populations. Ph.D. thesis, University of Cape Town. 248 p.

Andrew, P. A., and D. S. Butterworth. 1988. An examination of the effect of changes in mesh size on the catchability coefficient (*q*) and sustainable yield of the Southern African hake stocks. Collect. Sci. Pap. Int. Comm. SE Atl. Fish. 15(I): 23–45.

Angelsen, K. K., and S. Olsen. 1987. Impact of fish density and effort level on catching efficiency of fishing gear. Fish. Res. 5: 271–278.

Butterworth, D. S. 1988. Some recommendations regarding the assessment methodologies used by ICSEAF. Collect. Sci. Pap. Int. Comm. SE Atl. Fish. 15(I): 107–155.

Butterworth, D. S., and P. A. Andrew. 1987. Further results from the application of dynamic catch-effort models to the hake stocks in the ICSEAF convention area. Collect. Sci. Pap. Int. Comm. SE Atl. Fish. 14(I): 109–160.

Butterworth, D. S., M. O. Bergh, and P. A. Andrew. 1986a. A comparison of dynamic catch-effort model and VPA assessments for the hake stocks in ICSEAF divisions 1.3–1.6. Collect. Sci. Pap. Int. Comm. SE Atl. Fish. 13(1): 131–165.

Butterworth, D. S., M. O. Bergh, P. A. Andrew, and A. E. Punt. 1986b. Some aspects of management strategies for and the assessment of the hake stocks off southern Africa. Collect. Sci. Pap. Int. Comm. SE Atl. Fish. 13(1): 167–193.

Crawford, R. J. M., L. V. Shannon, and D. E. Pollock. 1987. The Benguela Ecosystem. Part IV. The major fish and invertebrate resources. Oceanogr. Mar. Biol. Annu. Rev. 25: 353–505.

Crecco, V., and W. J. Overholtz. 1990. Causes of density-dependent catchability for Georges Bank haddock *Melanogrammus aeglefinus*. Can. J. Fish. Aquat. Sci. 47: 385–394.

Deriso, R. B., P. R. Neal, and T. J. Quinn. 1989. Further aspects of catch-age analysis with auxiliary information, p. 127–135. *In* R. J. Beamish and G. A. McFarlane [ed.] Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models. Can. Spec. Publ. Fish. Aquat. Sci. 108.

Deriso, R. B., T. J. Quinn II, and P. R. Neal. 1985. Catch-age analysis with auxiliary information. Can. J. Fish. Aquat. Sci. 42: 815–824.

Draganik, B., and R. Sacks. 1987. Stock assessment of Cape hakes (*Merluccius capensis* and *M. paradoxus*) in the convention area. Divisions 1.3 + 1.4 Collect. Doc. Pap. Int. Commn SE. Atl. Fish. Doc. 18b.

Fox, W. W. 1974. An overview of production modelling, p. 142–156. *In* Proceedings of the ICCAT workshop on tuna population dynamics, Nantes, France, Sept. 1974.

Gordoa, A., and J. P. Pertierra. 1987. Catch fluctuations observed in the Cape hake fishery in division 1.5. Collect. Sci. Pap. Int. Comm. SE Atl. Fish. 14(I): 207–218.

Graham, M. 1935. Modern theory of exploiting a fishery and application to North Sea trawling. J. Cons. Int. Explor. Mer. 10: 264–274.

Gulland, J. A. 1977. The stability of fish stocks. J. Cons. Int. Explor. Mer 37: 199–204.

Hollowed, A. B., R. Methot, and M. Dorn. 1988. Status of the Pacific whiting resource in 1988 and recommendations to management in 1989. Appendix A in Status of the Pacific Coast groundfish fishery through 1988 and recommended acceptable biological catches for 1989. Pacific Fishery Management Council, Portland, OR.

Houghton, R. G., and S. Flatman. 1980. The exploitation pattern, density-dependent catchability, and growth of cod, *Gadus morhua*, in the west-central North Sea J. Cons. Int. Explor. Mer 39: 271–287.

Kimura, D. K. 1989. Variability, tuning, and simulation for the Doubleday–Deriso catch-at-age model. Can. J. Fish. Aquat. Sci. 46: 941–949.

MacCall, A. D. 1976. Density-dependence of catchability coefficient in the California Pacific sardine, *Sardinops sagax caerula*, purse-seine fishery. CalCOFI Rep. 18: 136–148.

1990. Dynamic geography of marine fish populations. University of Washington Press, Seattle, WA.

Macpherson, E., and B. Roel. 1984. Estudio del reclutamiento de la merluza en la divisions 1.4 y 1.5. Collect. Sci. Pap. Int. Comm. SE Atl. Fish. 11(1): 159–165.

Macpherson, E., B. Roel, and B. Morales. 1985. Reclutamiento de la merluza y abundancia y distribución de diferentes especies comerciales en las divisiones 1.4 y 1.5 durante 1983–1984. Collect. Sci. Pap. Int. Comm. SE Atl. Fish. 12: 1–61.

McLain, D. R., R. E. Brainard, and J. G. Norton. 1985. Anomalous warm events in eastern boundary current systems. CalCOFI Rep. 26: 51–64.

Methot, R., and J. Hightower. 1988. Status of the Washington–Oregon–California sablefish stock in 1988. Appendix B in Status of the Pacific Coast groundfish fishery through 1988 and recommended acceptable biological catches for 1989. Pacific Fishery Management Council, Portland, OR.

Murphy, G. 1965. A solution to the catch equation. J. Fish. Res. Board Can. 22: 191–202.

Paloheimo, J. E., and L. M. Dickie. 1964. Abundance and fishing success. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 155: 152–163.

Peterman, R. M., and G. Steer. 1981. Relation between sport-fishing catchability coefficients and salmon abundance. Trans. Am. Fish. Soc. 110: 585–593.

Pope, J. G., and D. J. Garrod. 1975. Sources of error in catch and effort quota regulations with particular reference to variation in the catchability coefficient. Int. Comm. Northwest Atl. Fish. Res. Bull. 11: 17–30.

Radovich, J. 1982. Catch-per-unit-of-effort: fact, fiction, or dogma. CalCOFI Rep. 18: 31–34.

Shannon, L. V., and S. C. Pillar. 1986. The Benguela ecosystem. Part III. Plankton. Oceanogr. Mar. Biol. Annu. Rev. 24: 65–170.

Shelton, P. A., and M. J. Armstrong. 1983. Variations in parent stock and recruitment of pilchard and anchory populations in the southern Benguela system. *In* G. D. Sharp and J. Csirke [ed.] Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San Jose, Costa Rica, April 1983. FAO Fish. Rep. 291(3): 1113–1132.

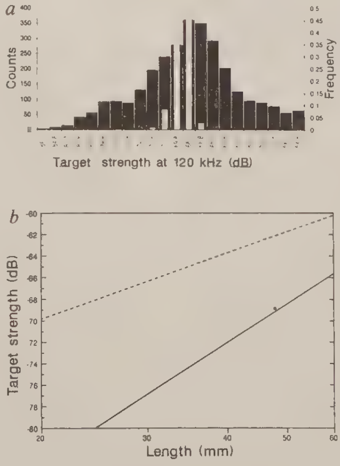
Winters, G. H., and J. P. Wheeler. 1985. Interaction between stock area, stock abundance, and catchability coefficient. Can. J. Fish. Aquat. Sci. 42: 989–998.

9135

Krill abundance

SIR — Antarctic krill (*Euphausia superba*) is the primary food source for many animals in the southern ocean and is also the basis of a large fishery. To manage this resource, krill abundance has been estimated directly with acoustics and indirectly with estimates of predator consumption rates. However, the abundance estimates using acoustics are often an order of magnitude less than those based on predator consumption rates[1]. The acoustic method converts echo energy to absolute biomass by assuming that the echo return is the sum of individual scatterers, and by assuming an empirical or modelled acoustic target strength (TS) for individual krill. Everson *et al.*[2] and Greene *et al.*[3] reported new TS measurements of experimentally constrained krill, but to date no corroborating field data have been published. We present new *in situ* TS measurements of krill obtained in March 1991 off Elephant Island, Antarctica.

Foote *et al.*[1] ensonified live krill aggregations in a cage at 120 kHz. The mean single-animal target strength of krill (lengths 30–39 mm) was inferred from the aggregation backscatter to range from −81 to −74 dB. Past acoustic surveys have typically used TS values calculated using the equations from the BIOMASS[4] program, but these equations lead to gross underestimates of krill abundance[2].



a, TS distribution for 2,957 individual krill detected with a Simrad EK500 echo sounder and a 120-kHz split-beam transducer off Elephant Island, Antarctica in March 1991. Solid bars, *in situ* measurements; open bars, distribution predicted from the sampled distribution of animal lengths. *b,* TS by length relationship at 120 kHz. Solid line reproduced from ref. 3. Also plotted are the median length and TS from the Foote *et al.* experiment (open circle)[1], the data reported here (solid circle), and the BIOMASS equation (dotted line).

Until recently, a fluid sphere model was thought to characterize adequately the acoustic TS of krill. Wiebe *et al.*[5] ensonified several species of live, but tethered, zooplankton at 420 KHz and concluded that sound scatter from elongated animals is better described by a bent cylinder model[6] and that TS is proportional to the volume of an animal rather than its cross-sectional area. Using these data, Greene *et al.*[3] predicted krill TS at several frequencies and over a range of animal lengths. The Foote *et al.* data agree with the TS prediction for a mean animal size of 33 mm. Because the bent cylinder model predicts that TS is much more sensitive to animal length than would be expected with the fluid sphere model, additional measurements of krill TS, particularly at different lengths, could provide strong corroboration of refs 1 and 3.

We present *in-situ* TS measurements of krill (mean length = 47.44 mm, $\sigma = 2.92$), around Elephant Island (*a* in the figure). Zooplankton sound scattering depends upon the morphology of the animal as well as its size, shape and orientation[5]. The spread of the distribution is likely due to the size distribution and variable orientation of the ensonified krill. Some of the high TS observations may be from multiple krill erroneously identified as individual scatterers. Nonetheless, the distribution is centred on −69dB, within 1dB of the prediction by Greene *et al.* Furthermore, the slope between the Foote *et al.* data and the data presented here is in accordance with that predicted by the bent cylinder model.

The TS of 47.44-mm krill estimated from the BIOMASS equations is −62.3 dB, 6.7 dB above the modal value of the measurements reported here. Thus, for a population composed of 47.44-mm individuals, abundance estimates using the mean TS reported here would be 4.7 times higher than that estimated with the BIOMASS value.

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1. Foote, K. G., Everson, I., Watkins, J. L. & Bone, D. G. *Acoust. Soc. Am.* **87**, 16–24 (1990).
2. Everson, I., Watkins, J. L., Bone, D. G. & Foote, K. G. *Nature* **345**, 338–340 (1990).
3. Greene, C. H., Wiebe, P. H. & McClatchie, S. *Nature*, **349**, 110 (1991).
4. Post-Fibex Acoustic Workshop *BIOMASS Report Ser.* No. 40 (1986).
5. Wiebe, P. H., Greene, C. H., Stanton, T. K. & Burczynski, J. *J. Acoust. Soc. Am.* **88**, 2346–2360 (1990).
6. Stanton, T. K. *J. Acoust. Soc. Am.* **86**, 1499 (1989).

HAZARDOUS AQUATIC ANIMALS 12

12.0 GENERAL

Many aquatic animals are potentially hazardous to divers. Although only a few present serious physical threats, the damage inflicted by others can seriously impair a diver's effectiveness. The material that follows discusses some of these animals. For convenience, hazardous aquatic animals have been classified as:

- those that abrade, lacerate, or puncture
- those that sting
- those that bite
- those that shock
- those that are poisonous to eat.

This classification has limitations: the categories overlap, and, although most hazardous species fall neatly into one or another, some of the classifications are arbitrary.

For a discussion of the treatment of injuries inflicted by hazardous aquatic organisms, see Section 18.

12.1 ANIMALS THAT ABRADE, LACERATE, OR PUNCTURE

The bodies of many aquatic animals are enclosed in sharp, pointed, or abrasive armor that can wound the exposed areas of a diver's body that come into forceful contact with these creatures. Included in this group of animals are such forms as **mussels, barnacles, sea urchins,** and **stony corals** (Figure 12-1). The wounding effect of contact between these animals and humans is intensified in aquatic habitats because human skin is softened by water. Although single encounters of this sort are unlikely to produce serious injury, repeated encounters during extended diving operations can produce multiple injuries that may become problems. Wounds continuously exposed to water resist healing, and careless divers may in time be incapacitated by an accumulation of ulcerated sores. Wounds are especially likely to be aggravated when working in the tropics. To compound the problem, secondary infections in such wounds are not uncommon. Thus, long-term diving projects can be crippled if participants fail to avoid these injuries, minor though they may initially seem.

Figure 12-1
Sea Urchin *Echinothrix diadema* on a Hawaiian Reef

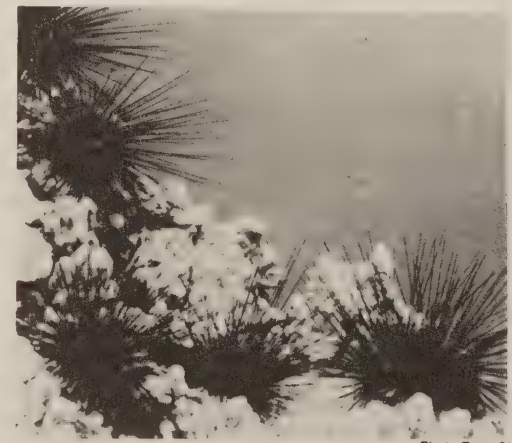


Photo Tony Chess

12.2 ANIMALS THAT STING—VENOMOUS MARINE ANIMALS

A diverse array of otherwise unrelated animals is considered together in this section because their ability to inject venom into other organisms poses a threat to divers in the water. The instrument of injection varies from the stinging cells of the coelenterates (hydroids, corals, anemones, and jellyfishes) to the spines on the bodies of crown-of-thorns starfish, sea urchins and fishes, radular teeth of cone shells, beaks of octopuses, bristles of annelid worms, and the fangs of snakes. Mere contact with the surface of some sponges can produce a severe dermatitis. The toxicity of the venom, as well as the amount of venom introduced, varies from one species to another and sometimes among individuals of the same species. Furthermore, humans may differ in their sensitivity to a given venom. The reactions of humans to marine animal stings may range from no noticeable reaction to mild irritation to sudden death. It is wise to become informed about and to avoid all marine organisms known to be venomous; occasional contact is inevitable, however, for even the most experienced divers.

12.2.1 Hydroids, Jellyfishes, Sea Anemones, and Corals

Grouped here are a variety of organisms that drift or swim slowly at the water's surface or at mid-depths.

They have gelatinous, semi-transparent, and often bell-shaped bodies from which trail tentacles armed with stinging cells, called nematocysts. In large specimens, these stinging tentacles may trail down as much as 100 feet into the water.

Nematocysts are characteristic of a large group of related, though superficially very diverse, marine animals known as **coelenterates.** In addition to the jellyfishes, the coelenterates also include the hydroids and stinging corals, considered below. Different coelenterates have different types of nematocysts, but all function similarly. When the animal is disturbed, the nematocyst forcefully discharges a venomous thread that, in some species, can penetrate human skin. The reactions of humans to the stings of hazardous coelenterates range from mild irritation to death.

Stinging hydroids occur on many reefs in tropical and temperate-zone seas. Typically, they are featherlike colonies of coelenterates (Figure 12-2) armed, like jellyfish, with nematocysts. Because colonies of these animals may be inconspicuous (they are often only a few inches high), they may go unnoticed. Except to the occasional person who is hypersensitive to their stings, hydroids generally are more of a nuisance than a hazard. Divers are most likely to be affected on the more sensitive parts of their bodies, such as the inner surfaces of their arms. Although clothing protects most of the body from the stings of hydroids, it will not protect against stings on the hands and face.

Stinging corals (Figure 12-3), often called fire coral, belong to a group of colonial coelenterates known as millepores. They are widespread on tropical reefs among the more familiar stony corals, which they superficially resemble. Contact with the nematocysts of millepores affects humans in about the same way as contact with the nematocysts of stinging hydroids. Common Florida and Bahama species have a characteristic tan-colored blade-type growth, with lighter (almost white) upper portions. *Millepora* may appear in the bladed or encrusting form over rock surfaces or on the branches of soft corals such as alcyonarians. The *Millepora* zone of the outer Florida Keys ranges from 10 to 25 feet deep.

Portuguese Men-o-War (Figure 12-4), which are grouped together in the genus *Physalia*, are colonial hydroids known as siphonophores. Siphonophores differ from the other forms considered here as jellyfish in that each organism is actually a colony of diverse individuals, each performing for the entire colony a specialized function such as swimming or capturing prey. A gelatinous, gas-filled float, which may be 6 inches or more in diameter, buoys the man-o-war at the surface, and from this float trail tentacles as long as 30 feet that bristle with nematocysts. Man-o-war stings can be dangerous to humans, so divers should stay well clear of these animals. Unfortunately, even the most careful diver can become entangled in a man-o-war tentacle, because these nearly transparent structures trail so far below the more visible float. It is

Figure 12-2
Stinging Hydroid

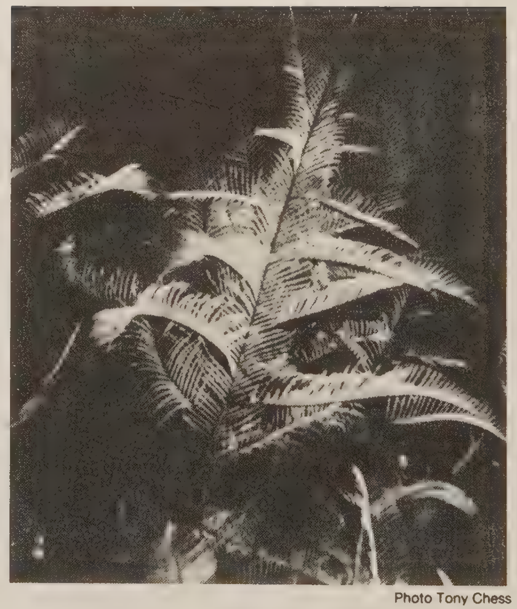


Photo Tony Chess

Figure 12-3
Stinging or Fire Coral

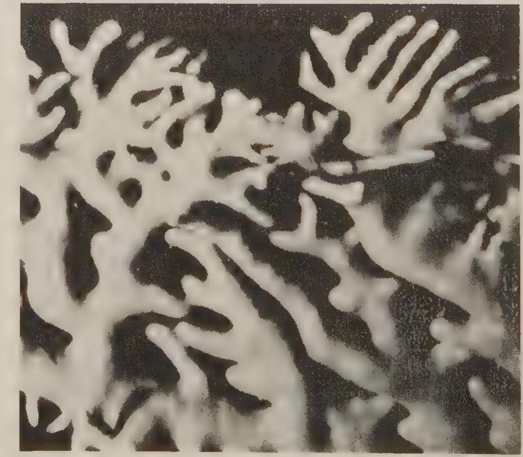


Photo Morgan Wells

Figure 12-4
Portuguese Man-of-War

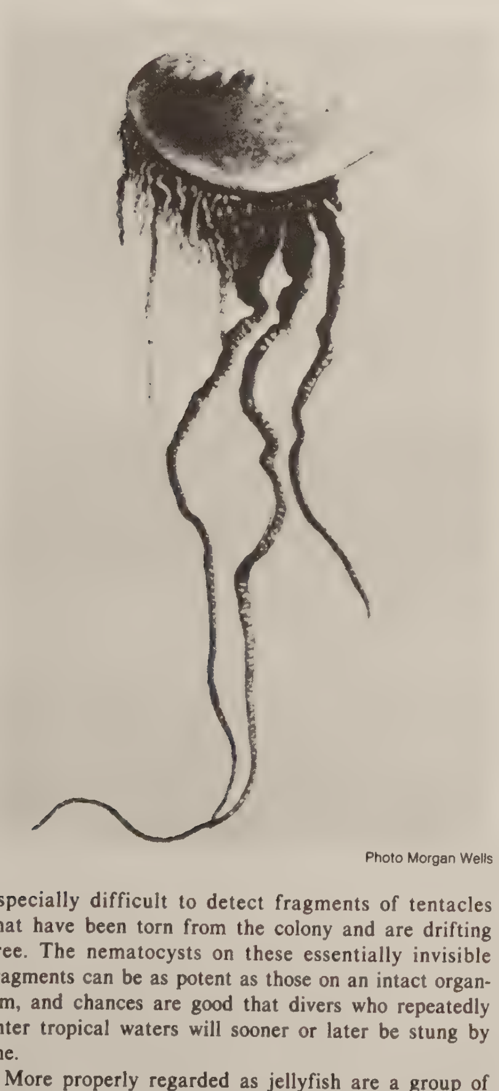


Photo Morgan Wells

Figure 12-5
Large Jellyfish of Genus *Cyanea*

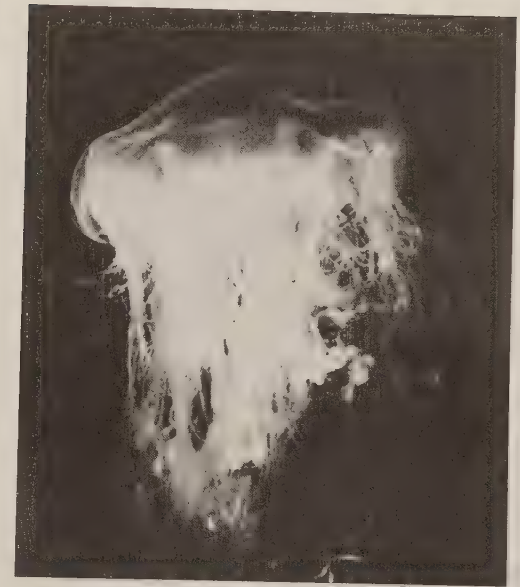


Photo Tony Chess

especially difficult to detect fragments of tentacles that have been torn from the colony and are drifting free. The nematocysts on these essentially invisible fragments can be as potent as those on an intact organism, and chances are good that divers who repeatedly enter tropical waters will sooner or later be stung by one.

More properly regarded as jellyfish are a group of coelenterates known as **scyphozoans**, each individual of which is an independent animal. These include the common jellyfishes encountered by divers in all oceans. Although many can sting, relatively few are dangerous. One large jellyfish of the genus *Cyanea* (Figure 12-5) is often encountered by divers in temperate coastal waters of both the Atlantic and Pacific oceans. Divers should be aware that there is a chance of being stung even after they leave the water, because segments of the tentacles of these animals may adhere to the diver's gloves, and touching the glove to bare skin, especially on the face, will produce a sting as painful as any received from the intact animal.

The most dangerous of the jellyfish belongs to a tropical subgroup of scyphozoans known as *cubomedusae*, or sea wasps. Sea wasps have an extremely virulent sting; one species in the southwest Pacific has caused death in humans. Fortunately, the more dangerous sea wasps are rarely encountered by divers.

Sea anemones of various species are capable of inflicting painful stings with their nematocysts. These animals frequently look like beautiful flowers, which may deceive people into touching them. The Hell's Fire sea anemone (*Actinodendron*), which is found in the Indo-Pacific region, is an example of such an anemone.

True corals are capable of inflicting serious wounds with their razor-sharp calcarious outer skeletons. Coral cuts are one of the most common hazards facing divers in tropical waters, and contact with corals should be carefully avoided. Divers should be equipped with leather gloves and be fully clothed when working among corals, because coral cuts, if not promptly and properly treated, can lead to serious skin infections.

12.2.2 Marine Worms

Marine worms that can be troublesome to divers are classified in a group known as polychaetes. Two types

Figure 12-6
Bristleworm

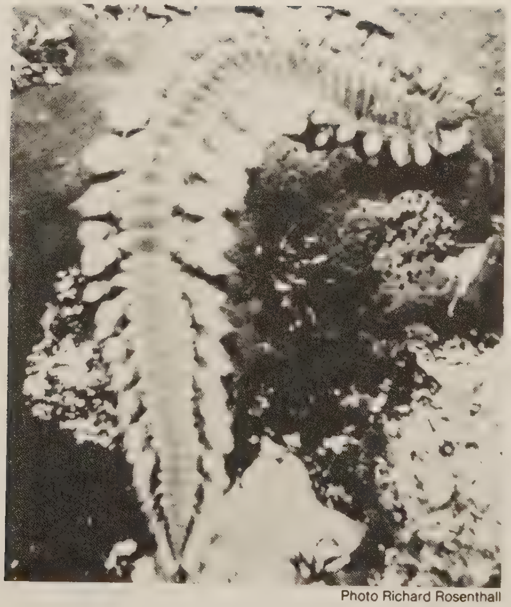


Photo Richard Rosenthall

reportedly inflict venomous wounds: bristle worms and blood worms.

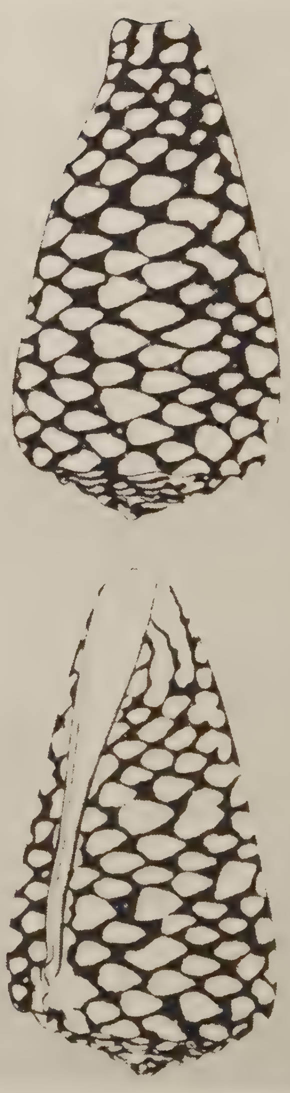
Bristleworms (Figure 12-6), which divers often encounter when overturning rocks, have tufts of sharp bristles along their segmented bodies that, in many species, can be extended when the animal is irritated. It has not been established that these bristles are venomous, but there is evidence for at least some species that this is so.

Blood worms burrow in mud or sand and some species can be a problem to divers who handle them. Their jaws contain venomous fangs, and their bite is comparable to a bee sting.

12.2.3 Cone Shells

Of the many diverse kinds of shelled mollusks in the sea, only some of the tropical cone shells are hazardous to divers (Figures 12-7 and 12-8). **Cone shells**, characterized by their conical shape, are an especially attractive hazard because collectors are drawn to the colorful shells of the most dangerous species. There are more than 400 kinds of cone shells, each with a highly developed venom apparatus used to stun the small animals that are its prey. The weapon of cone shells is thus an offensive rather than defensive one, a fact that helps to reduce the number of times people handling these shells are stung. Although only a relatively few of the cone shells are dangerous to divers, the stings of some can reportedly be deadly. Because cone shells inject their venom with a harpoonlike structure located at the narrow end of their shells, persons handling these animals should grasp them at the wide end.

Figure 12-7
Cone Shell



Source: NOAA (1979)

Figure 12-8
Anatomy of a Cone Shell

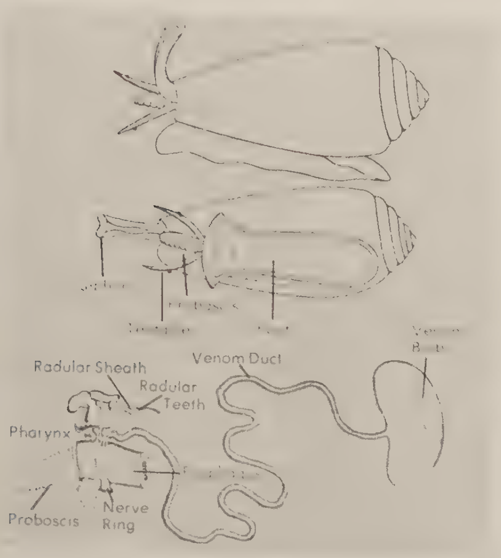


Photo Bruce W. Halstead

12.2.4 Octopuses

Octopuses are timid creatures that will take any opportunity to retreat from divers. Some species, however, can be hazardous to divers who attempt to handle them. When an octopus bites into prey with its parrotlike beak, venom enters the wound and subdues the prey. This venom normally is not toxic to humans, however. Although there have been relatively few cases of octopus bites in humans, one diver in Australia who allowed a rare blue-ring octopus to crawl over his bare skin was bitten on the neck and died within 2 hours. Because the bite of this species can be lethal, the Australian blue-ring octopus (Figure 12-9) should be carefully handled.

12.2.5 Sea Urchins

Among the more troublesome animals for divers working near tropical reefs are venomous **sea urchins**. This is especially true after dark, when visibility is reduced and many of the noxious sea urchins are more exposed than in daylight. Sea urchins may also be a problem in temperate waters, but the species in these regions lack the venom of the tropical species and therefore present a puncture rather than poisoning hazard.

Most difficulties with venomous sea urchins result from accidental contact with certain long-spined species. The smaller secondary spines that lie among the larger primary spines do the most damage; apart from their venom, these spines invariably break off in the wound and, being brittle, frequently cannot be completely removed. Gloves and protective clothing afford some protection against minor brushes with these animals but do not help much when a diver strikes forcefully against them. To avoid painful injury when working close to venomous sea urchins, divers should avoid contact.

Figure 12-9
Rare Australian Blue-Ring Octopus

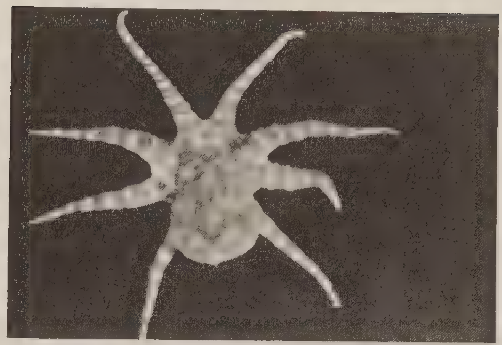


Photo Bruce W. Halstead

Some of the short-spined tropical urchins are reported to be hazardous because they have tiny pincerlike organs, called pedicellariae, that occur among their spines. Although some pedicellariae contain a potent venom, they are very small structures that probably do not threaten divers who incidentally come into contact with the urchins that carry them. When wearing gloves, one can handle these urchins without concern for their pedicellariae.

12.2.6 Fishes

Many fishes inflict venomous wounds. Most do so with their fin spines, but some wound with the spines located on their heads or elsewhere on their bodies. Generally these fishes injure only divers who deliberately handle or provoke them; however, some wound divers who unintentionally touch them or come too close.

Stingrays. Stingrays carry one or more spikelike spines near the base of their flexible tails, which they can use effectively against those who come in contact with them. Although these spines can inflict venomous puncture wounds similar to those of the fishes discussed above, they more often inflict a slashing laceration. Humans are most threatened when they are wading on sandy bottom in shallow water or swimming close to the bottom. Walking with a shuffling motion tends to frighten stingrays away. Stingrays are responsible for more fish stings than any other group of fishes. Species of the family Dasyatidae present the greatest danger, combining as they do large size, the habit of lying immobile on the seafloor covered with sand, and a large spine that is carried relatively far back (compared to those of other stingrays) on a whiplike tail (Figure 12-10). Large rays of this type can drive their spines through the planks of a small boat or through a human arm or leg. Swimmers coming into contact with the bottom have been mortally wounded when struck in the abdomen by a dasyatid stingray lying unseen in the sand.

The urolophid, or round, stingrays have a short muscular caudal appendage to which the sting is attached; they are thus able to deliver severe stings with a whip of their tail. Many of the most common stingray envenomations are caused by round stingrays.

Less dangerous are stingrays of the family Myliobatidae, which includes the bat rays and eagle rays (Figure 12-11), even though these animals can be large and have long venomous spines on their tails. The spines of these species are at the bases of their tails rather than farther back and so are far less effective weapons than the spines of the dasyatid or urolophid rays. The myliobatid rays are also less cryptic than the dasyatids or urolophids: rather than lying immobile on the bottom most of the time, they more often swim through the midwaters, their greatly expanded pectoral fins flapping gracefully like the wings of a large bird. When on the seafloor, myliobatid rays usually root actively in the sand for their shelled prey, and thus are readily seen.

Scorpionfishes. Scorpionfishes are among the most widespread and numerous family of venomous fishes. The family, which numbers several hundred near-shore species, has representatives in all of the world's seas, but the most dangerous forms occur in the tropics. Scorpionfishes usually inject their venom with their dorsal fin spines and less often do so with the spines of their anal and pelvic fins.

Many scorpionfishes are sedentary creatures that lie immobile and unseen on the seafloor. An example is the **sculpin**, a common near-shore scorpionfish species of southern California. Another example, the **stonefish**, is common in the shallow, tropical waters of the western Pacific and Indian Oceans; this species has the most potent sting of all scorpionfishes and has caused deaths among humans. Although stonefish are not aggressive toward divers, their camouflage makes it easy to step on them unless special care is taken.

In contrast to the cryptic sculpin and stonefish, another group of scorpionfishes, the brilliantly hued **lionfishes**

Figure 12-10
Dasyatid Stingray

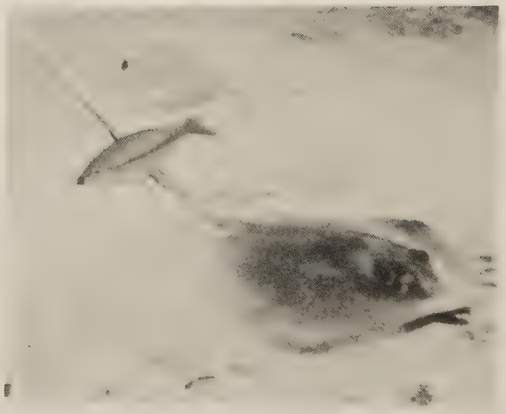


Photo Morgan Wells

Figure 12-11
Myliobatid Stingray

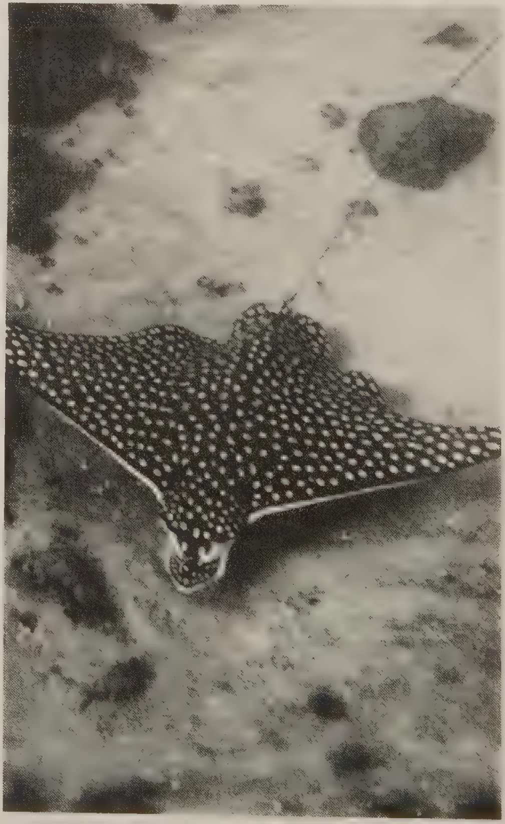


Photo Edmund Hobson

Figure 12-12
Lionfish

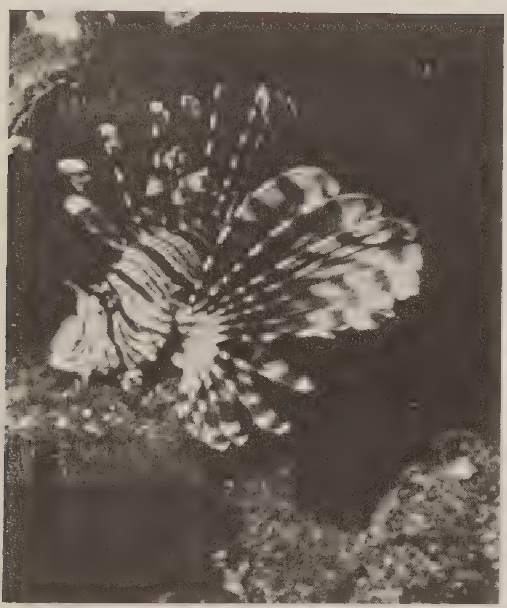


Photo Al Giddings

Figure 12-13
Surgeonfish

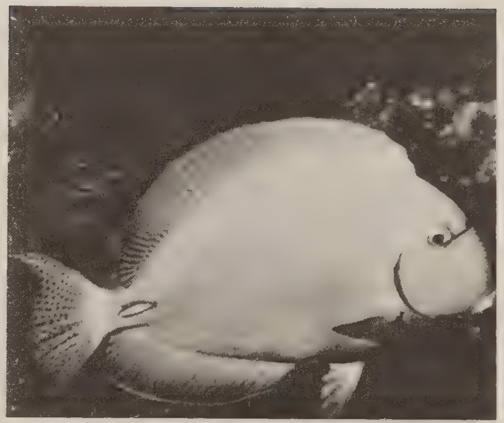


Photo Edmund Hobson

(Figure 12-12), stand out strikingly against their surroundings. Because lionfishes are beautiful animals that make little effort to avoid humans, inexperienced divers may be tempted to grasp hold of one. This could prove a painful mistake, because lionfish venom is especially potent.

Other fishes similarly armed with venomous fin-spines include: the **spiny dogfish**, family Squalidae; **weever fishes**, family Trachinidae; **toadfishes**, family Batrachoididae; **stargazers**, family Uranoscopidae; **freshwater** and **marine catfishes**, family Ariidae; **rabbitfishes**, family Siganidae; and **surgeonfishes**, family Acanthuridae. These fishes do not usually generate sufficient force to drive their venom apparatus into their victims; instead, the force is supplied by the victims themselves, who handle or otherwise come into contact with these fishes. A number of fishes, however, do actively thrust their venom apparatus into their victims, an action that often produces a deep laceration; fishes of this type are discussed next.

Surgeonfishes. As noted above, some surgeonfishes (Figure 12-13) can inflict venomous puncture wounds with their fin spines; these wounds are much like those produced by scorpionfishes and other similarly armed fishes. Many surgeonfishes can also inflict deep lacerations with knifelike spines they carry on either side of their bodies, just forward of their tails. Although not conclusive, there is evidence that these spines are venomous in at least some species. The more dangerous surgeonfishes, which belong to the genus *Acanthurus*, usually carry these spines flat against their bodies in integumentary sheaths; however, when threatened, these fish erect these spines at right angles to their bodies and attack their adversaries with quick, lashing movements of their tails. Divers injured by surgeonfishes have usually been hurt while trying to spear or otherwise molest them.

12.2.7 Reptiles

Venomous snakes are a more widespread hazard in fresh water than in the sea. The **cottonmouth water snake**, which has an aquatic bite known to have been fatal to humans, may be the most dangerous animal hazard that divers face in fresh water. This species, which is difficult to identify because of its highly variable coloration, does not show the fear of humans that is characteristic of most aquatic snakes. In regions inhabited by the cottonmouth, divers should avoid any snake that does not retreat from them. The best defense is a noiseless, deliberate retreat. Wet suits afford reasonably good protection but can be penetrated by the teeth of larger specimens. The diver should not attempt to strike back, since this practice may result in multiple bites. Although the evidence is not conclusive, the snake is believed not to dive deeper than about 6 feet. Another species to avoid is the **timber rattlesnake**, an excellent swimmer at the surface. Venomous **sea snakes** occur only in tropical regions of the Pacific and Indian oceans. These reptiles have a highly virulent venom, but fortunately for divers they generally do not bite humans unless roughly handled. Sometimes a sea snake that is caught amid a netload of fishes will bite a fisherman, but generally they are not aggressive toward divers who meet them under water. Sea snakes are especially numerous in the waters near the East Indies. Sea snakes are the most numerous of all reptiles and are sometimes seen in large numbers in the open ocean. Divers most often see them amid rocks and coral, where they prey on small fishes (Figure 12-14). They are agile underwater swimmers, and divers should not lose respect for their deadly bite simply because they are reportedly docile.

12.3 ANIMALS THAT BITE

Serious injuries caused by the bites of non-venomous marine animals are rare. However, the possibility of such injury is psychologically threatening, partly because this hazard has been so widely publicized that many divers are distracted by it. It is important that working divers view this hazard realistically.

12.3.1 Fishes

Sharks have been given more sensational publicity as a threat to divers than any other animal, even though shark bites are among the most infrequent of all injuries that divers sustain in the sea. This notoriety is understandable; injuries from shark bites generally are massive and are sometimes fatal. Nevertheless, only a very few of the many species of sharks in the sea threaten humans.

The vast majority of sharks are inoffensive animals that threaten only small creatures like crabs and shellfish. However, some sharks that are usually inoffensive will bite divers who are molesting them; included here are such common forms as **nurse sharks** (family Orectolobidae) and **swell sharks** (family Scyliorhinidae). These animals appear docile largely because they are so sluggish, but large specimens can seriously injure a diver. Although any large animal with sharp teeth should be left alone, the sharks discussed below may initiate unprovoked attacks on divers.

Most sharks known to attack humans without apparent provocation belong to one of four families: the Carcharhinidae, which include the **gray shark**, **white-tip shark**, **blue shark**, and **tiger shark**; the Carchariidae, which include the **sand shark** (including the species called grey nurse shark in Australia, not to be confused with the animals called nurse sharks in American waters); the Lamnidae, which include the **mako shark** and **great white shark** (Figure 12-15); and the Sphyrnidae, which include the **hammerheads**. All of these are relatively large, active animals whose feeding apparatus and behavior give them the potential to injure divers seriously. Except for the hammerheads, whose name well characterizes their appearance, these sharks all look much alike to the untrained eye. The characteristics distinguishing them would certainly not impress most divers encountering them under water.

Figure 12-14
Sea Snake

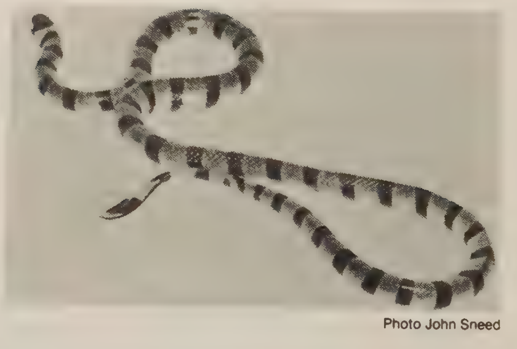


Photo John Sneed

Figure 12-15
Great White Shark

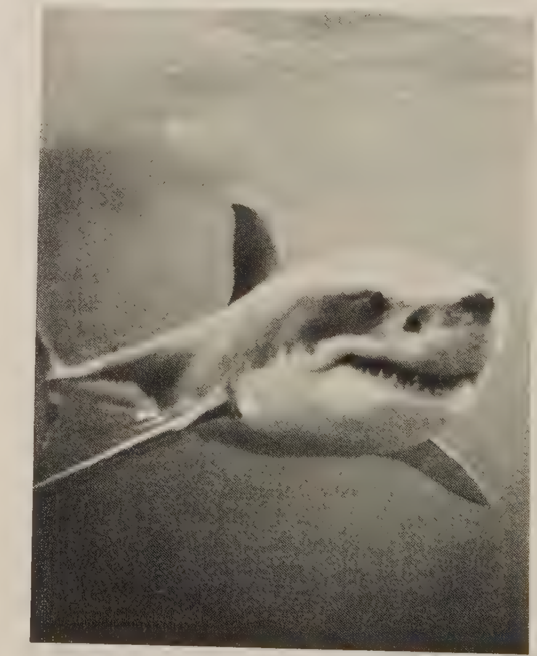


Photo Ron and Valerie Taylor

Figure 12-16
Gray Reef Shark

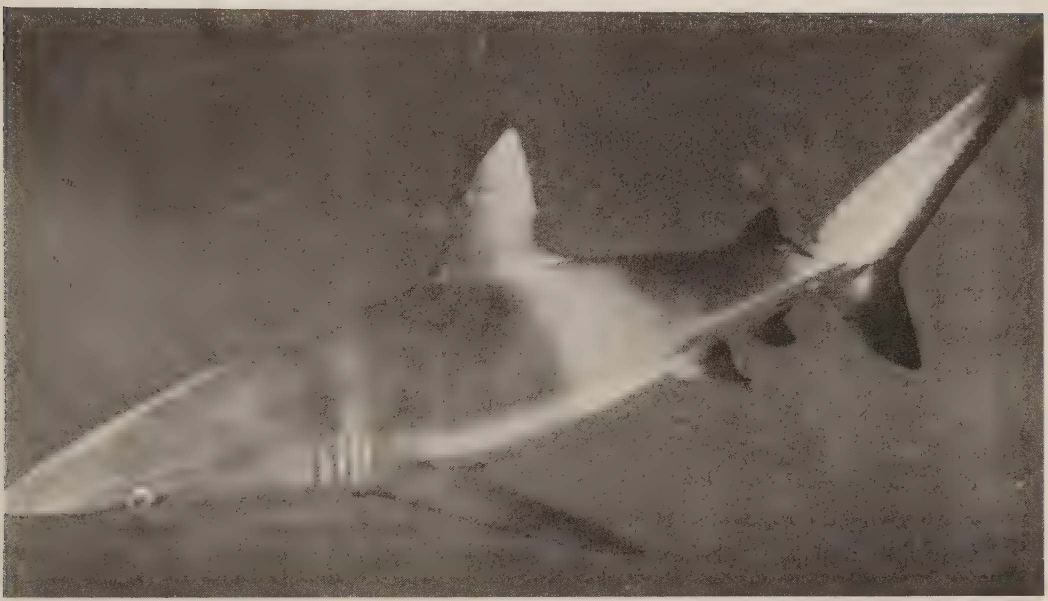


Photo Edmund Hobson

The **great white shark** is reputed to be the most dangerous of all sharks. This shark is credited with more attacks on humans than any other shark species. It attains a length of 20 feet or more.

The **gray reef shark** (Figure 12-16), numerous on tropical Pacific reefs, is typical of these potentially dangerous species. These sharks have repeatedly been incriminated in human attacks. Any creature over about 3 feet long that generally resembles this animal should be regarded cautiously, and if over about 8 feet long, it should be avoided—even if this requires the diver to leave the water. Sharks of these species that range between 3 and 7 feet in length are numerous in shallow tropical waters, and diving operations often cannot be performed unless the presence of sharks in the area is tolerated. When such sharks are in the vicinity, divers should avoid making sudden or erratic movements. Common sense dictates that no injured or distressed animals should be in the water, because these are known to precipitate shark attacks. When operations are conducted in the presence of sharks, each group of divers should include one person who keeps the sharks in view and is alert for changes in their behavior. The chances of trouble are minimal as long as the sharks swim slowly and move naturally. However, the situation becomes dangerous as soon as the sharks assume unnatural postures, such as pointing their pectoral fins downward, arching their backs, and elevating their heads. The moment sharks show such behavior, divers should leave the water. Gray reef sharks are sometimes encountered in large numbers, and when in large groups they may become very aggressive if food is in the water.

Moray eels (Figure 12-17) are a potential hazard on tropical reefs, and a few species occur in the warmer temperate regions of California and Europe. They are secretive animals, with body forms highly specialized for life within reef crevices; they are only rarely exposed on the reef top. Although relatively few grow large enough to threaten divers seriously, some attain a size greater than 5 feet. The moray's powerful jaws, with long needlelike teeth, can grievously wound humans.

Divers injured by morays have usually been bitten when they are reaching into a reef crevice for some object; they were struck by a moray that probably felt threatened or perhaps mistook the diver's hand for prey. The moray will usually release its grip when it recognizes that it has taken hold of something unfamiliar, and if divers can resist the impulse to pull free, they may escape with no more than a series of puncture wounds. But such presence of mind is rare in such a situation, and divers often receive severe lacerations when wrenching their hands from between the backward-pointing teeth of the eel.

Figure 12-17
Moray Eel

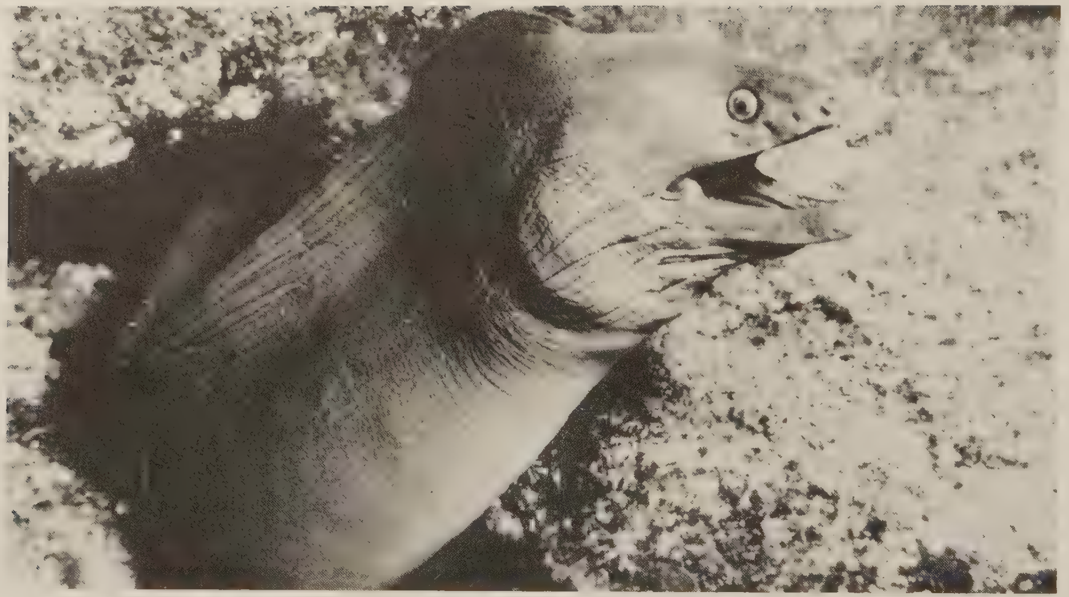


Photo Edmund Hobson

Barracudas (Figure 12-18) are potentially dangerous fishes that occur widely in the coastal waters of tropical and subtropical seas. Often exceeding 4 feet in length and with long canine teeth in a large mouth, these fishes have the size and equipment to injure humans severely. Large barracuda often follow divers about, apparently to get a good look at the divers; it is important to remember that even the smallest diver is much larger than anything the barracuda is accustomed to eating. The barracuda's teeth are adapted for seizing the fish that are its prey; however, these teeth are ill-suited to tearing pieces from an animal as large as a human. Attacks on divers are most likely to occur where the barracuda has not had a good look at its victim. Where visibility is limited, for example, the barracuda may see only a moving hand or foot, which may be mistaken for prey. An attack may also occur when a diver jumps into the water, as when entering the sea from a boat. To a nearby barracuda, the diver's splash may simulate the splash of an animal in difficulty—and hence vulnerable—and the barracuda may strike without realizing what made the splash. Thus one should be especially alert in murky water to avoid unnecessary splashing when large barracudas may be present.

Other fishes that bite. Any large fish with sharp teeth or powerful jaws can inflict a damaging bite. Generally, however, such fish are hazardous to divers only when they are handled. The **pufferfishes**, **wolffishes**, and **triggerfishes** can be especially troublesome in this respect. These fishes have teeth and jaws adapted to feeding on heavily armored prey, and large specimens are quite capable of biting off a human finger.

In the tropics, some of the larger **sea basses** can grow to more than 7 feet. These giant fish, including certain **groupers** and **jewfishes**, are potential hazards. Their mouths can engulf a diver, and there are reports that they have done so.

12.3.2 Reptiles

Reptiles that bite, including turtles, alligators, and crocodiles, are potential hazards to divers, both in freshwater and in the sea.

Turtles are frequently encountered by divers; however, although the larger individuals of some species can injure divers with their bites, these animals are not generally threatening. Although the larger marine turtles have occasionally inflicted minor injuries, several freshwater species are far more vicious and aggressive; these include the alligator snapping turtle and common snapping turtle of American fresh waters. The softshell turtle also may inflict a serious wound.

Figure 12-18
Barracuda

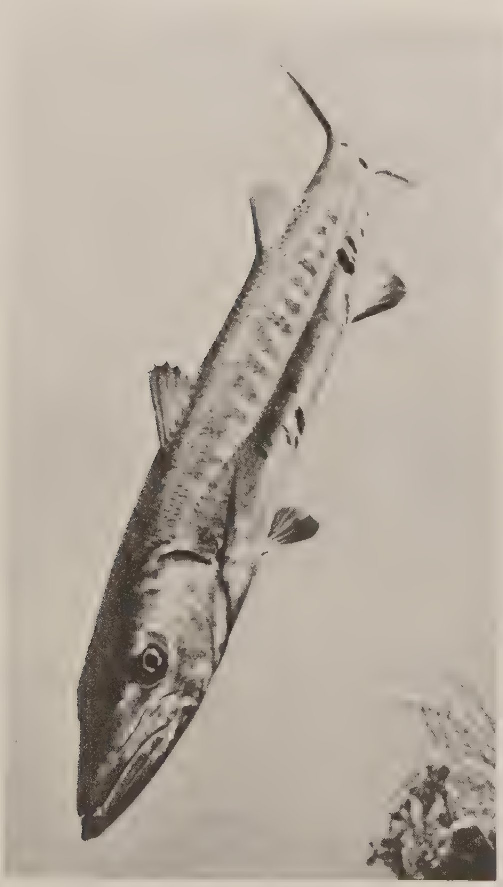


Photo Dick Clarke

Alligators that have been encountered by divers, including the American alligator, have not proved threatening. Nevertheless, the potential for serious injury exists, and divers should be cautious.

Crocodiles are more dangerous than alligators. A species in the tropical western Pacific that enters coastal marine waters is feared far more than sharks by the natives, and with good reason: it is known to have attacked and eaten at least one diver.

12.3.3 Aquatic Mammals

Juvenile and female **seals** and **sea lions** frequently frolic in the water near divers. Underwater encounters with sea lions can be expected if the animals are nearby during a dive. Their activity can be distracting or even frightening, but it is rarely dangerous. Large bull seals and sea lions, although aggressive on the above-water rocks of their breeding rookery, apparently do not constitute a serious threat under water. A potentially greater danger when swimming with seals is being shot by a person hunting illegally. Some divers wear bright markings on their hoods for this reason. If bitten by a seal or sea lion, the diver should consult a physician, because some species may transmit diseases that are infectious among humans.

Common sense dictates that divers avoid large **whales** under water. Usually whales stay clear of divers, so that most incidents occur when divers put themselves in jeopardy by provoking the whales. Whales may be startled when a diver approaches too close and may strike a diver senseless in their sudden surge of evasive action.

Muskrats are potential hazards in fresh water. Usually they attack only if they believe themselves to be threatened; their bites produce only minor wounds. However, there is a serious danger that rabies can be contracted from muskrat bites, so in addition to seeking immediate medical advice, divers who are bitten should make every effort to capture or kill the animal for later examination.

12.4 ANIMALS THAT SHOCK

Among marine animals that produce an electric shock, the only one significantly hazardous to divers is the **electric ray**, which has representatives in all the oceans of the world. The **torpedo ray** of California (Figure 12-19), which can grow to 6 feet in length and weigh up to 200 pounds, is an example. These rays are shaped somewhat like a stingray, except that their "wings" are thick and heavy and their tails are flattened for swimming. Electric rays are slow-moving animals, and alert divers should have little trouble avoiding them. As is true of so many undersea hazards, these animals generally threaten only those divers who molest them. The electric ray's shock, which can be as large as 200 volts, is generated by modified muscles in the forward part of the animal's disc-shaped body. The shock, which is enough to electrocute a large fish, can jolt a diver severely.

12.5 ANIMALS POISONOUS TO EAT

Most seafoods are edible and nourishing; however, several of the most toxic substances known are sometimes found in marine organisms. Mollusk shellfish, such as clams, mussels, and oysters, are sometimes poisonous to eat. These shellfish become poisonous because they feed on toxic dinoflagellates, which are

Figure 12-19
Torpedo Ray

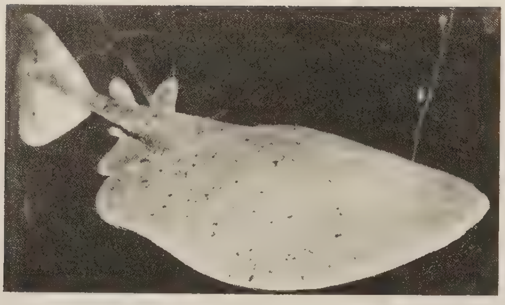


Photo Tony Chess

microscopic plankton. Most of these episodes of poisoning have occurred along the Pacific coast from California to Alaska; the northeast coast from Massachusetts to Nova Scotia, New Brunswick and Quebec; and in the North Sea countries of Britain and West Germany. It is advisable to check with local authorities to determine what periods are safe for eating mollusk shellfish. Violent intoxications and fatalities have also been reported from eating tropical reef crabs; these should not be eaten without first checking with the local inhabitants. Numerous species of tropical reef fishes are known to be poisonous to eat because they cause a disease known as ciguatera (see Section 18 for a discussion of ciguatera poisoning treatment). An edible fish in one locality may be deadly in another.

Figure 12-20
Examples of Pufferfish

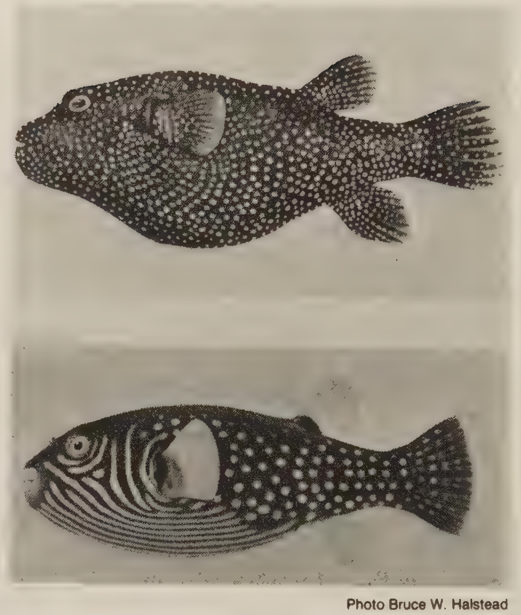


Photo Bruce W. Halstead

In addition, most pufferfish (Figure 12-20) contain a deadly poison known as tetrodotoxin, and puffers and related species should be carefully avoided.

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CHAPTER 4

Trophic Relationships of Fishes Specialized to Feed on Zooplankters above Coral Reefs

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I. INTRODUCTION

Fishes specialized to feed on zooplankters are major components of coral reef communities. They are distinctive animals, with many features that relate to their way of feeding. Although most fishes are planktivorous as larvae and early juveniles (Durbin, 1979), generally only species with appropriate adaptations remain obligate planktivores as adults (Davis and Birdsong, 1973; Hobson and Chess, 1976, 1978). This chapter examines how these species have accommodated the special needs of planktivory while retaining close ties to reef structures, generally as places to shelter when at rest or threatened.

Virtually all coral reef planktivores are among the highly diverse acanthopterygians (spiny-finned teleosts), which are the most highly evolved fishes (Gosline, 1971). Acanthopterygians dominate in coral reef communities (Smith and Tyler, 1972, Schaeffer and Rosen, 1961); for example, 98% of the species noted during a census of Hawaiian reefs are members of this group (Hobson, 1974).

Despite the great diversity of forms among coral reef acanthopterygians, however, virtually every major family includes species that are specialized as planktivores. For example, there are diurnal planktivores among the Serranidae, Chaetodontidae, Pomacentridae, and Balistidae, and there are nocturnal planktivores among the Holocentridae, Priacanthidae, and Apogonidae (Starck and Davis, 1966; Randall, 1967; Hobson, 1974). Most planktivorous acanthopterygians, including all species considered in this chapter, feed with visually oriented strikes at individual prey (Zaret, 1972; Confer and Blades, 1975; Durbin, 1979; unpublished observations). Furthermore, the major threats to planktivores feeding above coral reefs (at least during the day) come

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from visually oriented attacks of large piscivorous fishes (Hobson, 1968, 1972). With vision so important, the trophic relations of coral reef planktivores—both as predators and as prey—are profoundly influenced by variations in levels of incident light (Hobson, 1972; Stevenson, 1972; Collette and Talbot, 1972). Many are adapted to specific photic conditions (Hobson, 1972; Munz and McFarland, 1973) and the vast majority feed strictly by day or by night (Hobson, 1974, 1975).

A. Need for Innovative Methods of Study

Studies of trophic dynamics among fishes and zooplankters above coral reefs have required innovative sampling procedures. The traditional methods used to sample zooplankton, for example, were developed for work in open water offshore and are ineffective in confined spaces among reefs. So studies that would sample coral reef plankton have used nets pushed by divers (Emery, 1968; Hobson and Chess, 1978) and tethered to anchors on the reef (Johannes *et al.,* 1970; Hobson and Chess, 1978). And traps have been set on the seabed to sample the many otherwise benthic organisms that periodically join the plankton (Porter and Porter, 1977; Alldredge and King, 1977, 1980; Hobson and Chess, 1979, 1986). Similarly, assessments of trophic relations among fishes based on specimens collected from above water are limited by problems of relating gut contents to occurrences of organisms in the environment. To better define prey selection by planktivorous fishes, hand-held spears have been used to select specimens known to have been feeding at the specific time and place where the plankton was sampled (Hobson, 1968; Hobson and Chess, 1976, 1978).

Perhaps the greatest advantage these methods have over traditional shipboard operations for study of trophic interactions, however, is that they put the investigator at the site of the interactions. From there one can directly observe vital spatial and temporal relationships and behaviors that can only be inferred from above water. These methods and advantages, with emphasis on events throughout day and night, have been refined by my studies with James R. Chess of interactions among reef fishes and zooplankters at widespread locations in the Atlantic and Pacific oceans. This chapter incorporates data, observations, and impressions gained from these studies in a synthesis of present knowledge.

II. DIURNAL PLANKTIVORES

Planktivorous reef fishes that feed by day typically form aggregations in the water column (Fig. 1), and from a distance it is often difficult to distinguish one species from another. Despite differing limitations on adaptive change

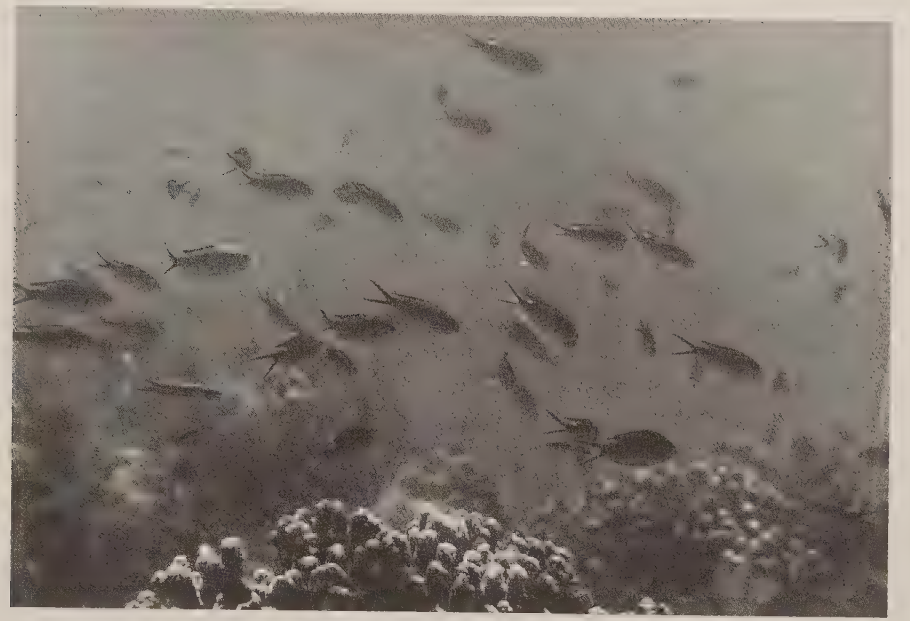

Figure 1 Feeding aggregation of *Chromis atrilobata* (Pomacentridae), a diurnal planktivore in the Gulf of California, Mexico.

related to their differing phylogenies, these fishes have acquired similar features in response to problems they have in common. This is especially evident in adaptations to the size of their prey and to feeding in exposed positions above the reefs. As a result of the remarkable degree of morphological and behavioral convergence that has developed, they tend to resemble one another more than they do other members of their own families that feed on the benthos (Davis and Birdsong, 1973).

A. Adaptations to a Diurnal Planktivorous Diet

Most diurnal reef planktivores feed primarily on swimming crustacea, particularly calanoid and cyclopoid copepods, but larvaceans or fish eggs are favored by some (Hiatt and Strasburg, 1960; Hobson and Chess, 1978; Sano *et al.*, 1984b). These prey vary in form and behavior, but those accessible during the day are largely transparent and visible mainly through their pigmented parts, such as eyes, or even gut contents (Zaret, 1980). So while planktivorous fishes generally take the larger of zooplankters available to them (Ivlev, 1961; Coates, 1980), they have been known to take the smaller of two similar forms if this one is more heavily pigmented (e.g., Zaret, 1972; Zaret and Kerfoot, 1975).

Whatever problems there may be with pigmentation, however, clearly it is an advantage to be smaller (Hobson and Chess, 1976; Obrien, 1979). And so zooplankters above coral reefs during the day tend toward not only transparency, but also reduced size. Judging from my studies with Chess, virtually all zooplankters taken by planktivorous reef fishes during the day are less than 3 mm in their greatest dimension.

Because planktivorous reef fishes have evolved from early ancestors that were adapted to feed on relatively large prey (Schaeffer and Rosen, 1961; Gosline, 1971), successful feeding depends on the performance of features modified for tasks very different from their original purpose. Particularly important have been modifications of head and jaws, including dentition, that permit even relatively large individuals to consume tiny organisms in open water. In contrast to the large, generalized mouth of the ancestral form (Gosline, 1971), most diurnal planktivores have a small mouth that in many is sharply upturned and with highly protrusible, often toothless jaws (Davis and Birdsong, 1973). Thus, whereas the primitive mouth functioned to grasp large prey, the modern planktivore mouth functions to engulf small prey.

Most of the evolution from the primitive condition, however, occurred in nonplanktivorous progenitors of modern planktivores. Protrusible jaws, for example, characterized the early acanthopterygians (Alexander, 1967; Gosline, 1971) and are now widespread among fishes (see Motta, 1984, for a review). As Gosline (1981, p. 11) stated: "The acanthopteran (acanthopterygian) system of premaxillary protrusion . . . appears to form part of the inheritance of all higher teleosts." It was to a large extent the potential of this feature that led Schaeffer and Rosen (1961, pp. 198–199) to state: "It is primarily the acanthopterygian mouth that has given rise to the enormous variety of specialized . . . feeding mechanisms for which teleosts are so well known." Among these specialized feeding mechanisms are those of diurnal planktivores, which have been refined by selection pressures specific to the planktivorous habit.

So even though some of the most protrusible jaws occur in such nonplanktivorous forms as the piscivorous *Luciocephalus pulcher* (Lauder and Liem, 1981) and the benthivorous *Gerres* spp. (Schaeffer and Rosen, 1961), the feature has nevertheless proven especially adaptive in planktivory. For example, when pomacentrids of the planktivorous genus *Chromis* are within a few centimeters of a target, their jaws shoot forward and engulf the prey (Fig. 2). According to Davis and Birdsong (1973, p. 299), jaw protrusion in planktivores "creates suction which draws prey into the cavity." This view is consistent with Lauder and Liem's (1981, p. 266) assessment that "an underlying assumption of most current research on advanced teleost feeding mechanisms is that protrusion is correlated with increased suction efficiency." But Lauder and Liem went on to show that the extremely protrusible jaws of *Luciocephalus pulcher* (among the most protrusible in teleosts) produce very little suction.

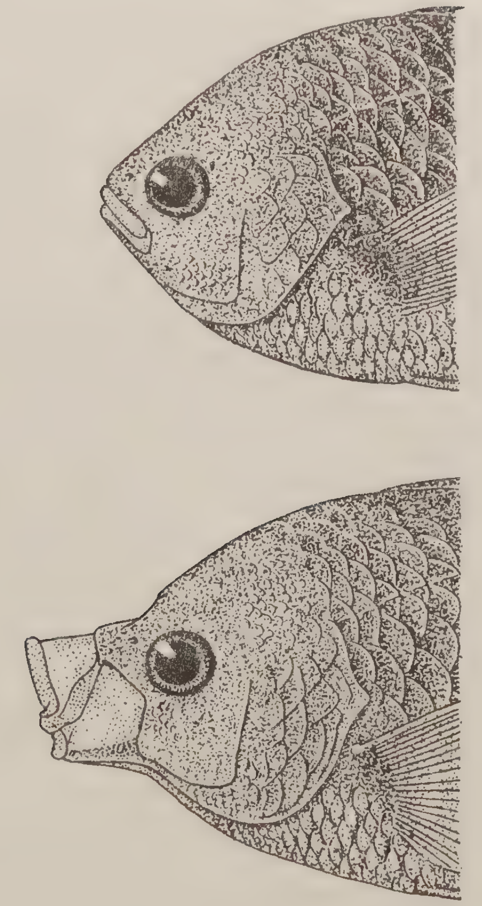

Figure 2 The protrusible upper jaw of *Chromis punctipinnis*, a typical feature of diurnal planktivores, permits projecting the mouth to engulf prey without swimming forward.

The assumption that jaw protrusion functions mainly to produce suction was earlier questioned by Nyberg's (1971) study of feeding mechanics in *Micropterus salmoides* (Centrarchidae). That species, Nyberg concluded, uses protrusion less to create suction than to bring the jaws more quickly to the prey. The advantage is greatest, he observed, in smaller bass moving slowly during the attack, and he related this to a trend in acanthopterygian evolution in which smaller, more protrusible mouths are associated with slower approaches to prey. Certainly planktivorous fishes above tropical reefs represent a culmination of this trend. *Chromis* spp., for example, generally move little, if at all, toward their prey; instead, they depend largely on their extremely protrusible jaws to get their mouths to the target. This is the "ram-jaw" feeding mode described by Coughlin and Strickler (1990), who used high-speed cinemaphotography and video to analyze feeding by *Chromis viridis*. They concluded that this species uses "ram-jaw," low-suction feeding to capture evasive prey, but decreases jaw protrusion and increases suction when prey are less evasive.

Although the small mouth is another planktivore feature widespread among nonplanktivores, the oblique orientation of this mouth, so common among planktivores, seems to be a feature especially adaptive in fishes that would capture tiny, motile organisms in open water. Probably the advantage of this arrangement comes not from the orientation of the mouth, but rather as a consequence of the shortened snout, which places both eyes in position to train simultaneously on small targets immediately ahead (W. A. Starck, cited in Rosenblatt, 1967a).

Gill rakers, a general feature of acanthopterygians that prevents ingested prey from escaping through the gill openings, tend in planktivores to be long and especially numerous (thus closely spaced). This increases their effectiveness in fishes that would feed on small prey (Davis and Birdsong, 1973).

Despite these adaptive tendencies, however, trophic features vary among planktivores—even among close relatives. The mechanisms and structures involved in jaw protrusion, for example, vary among species of *Chromis* (Emery, 1973). So while similarities related to their common purpose unite the group, each species has been to some varying extent customized by distinctive elements of its evolutionary history.

B. Adaptations to Diurnal Threats from Predators

Interspecific convergence among diurnal planktivorous fishes in features that increase mobility are even more striking than the convergence in features that enhance feeding. Particularly evident are tendencies toward streamlined bodies and deeply forked caudal fins—features that increase swimming speeds (Norman, 1947). Significantly, these features generally are more developed in fishes that range farther from the reef (Fig. 3), which indicates an increasing need for swimming efficiency in open water. Consistent with this is a tendency to be larger, which might be expected considering the direct relation between body length and swimming speed.

Planktivores that forage farther above the reef would find that streamlining helps them maintain station in the stronger currents that flow there. They would also benefit from a speedy flight to the reef, because the survival of small fishes exposed to predators in sunlit open water often depends on how fast they get to shelter when threatened (Hartline *et al.*, 1972; Hobson and Chess, 1978).

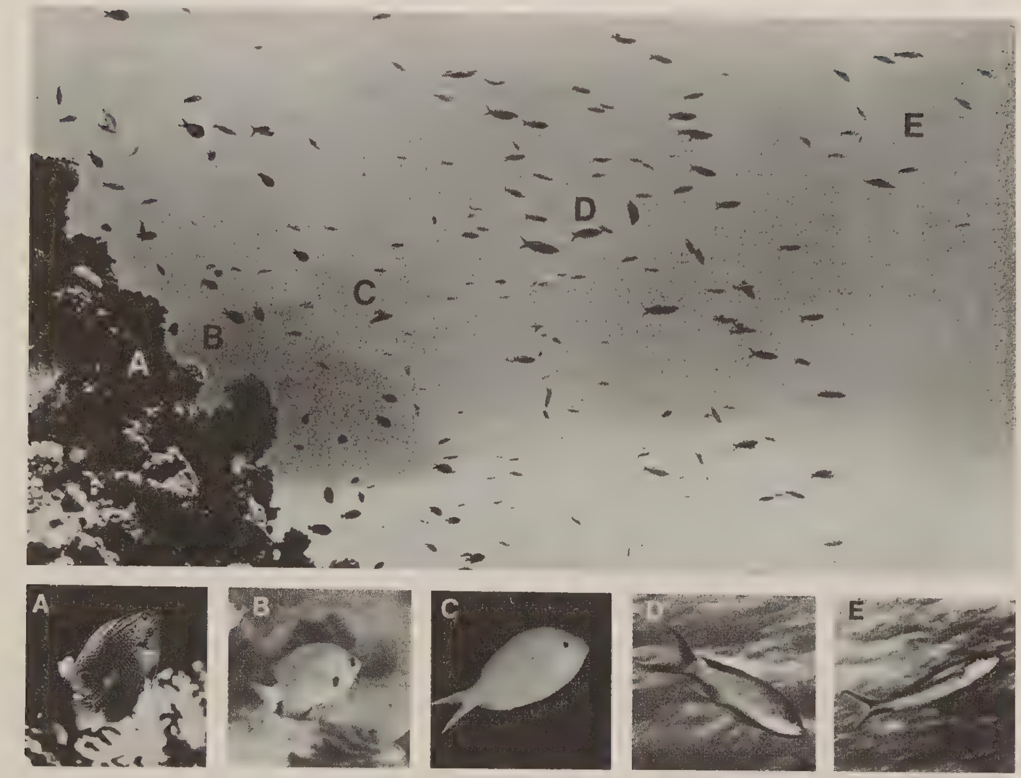

Figure 3 Planktivorous fishes foraging above a reef in the lagoon of Enewetak Atoll. Note that those farther from the reef have features that increase their swimming speed and ability to maintain station in currents. (A) *Pomacentrus vaiuli,* (B) *Chromis agilis,* (C) *Chromis viridis,* (D) *Anthias pascallus,* (E) *Pterocaesio tile.*

Diurnal planktivorous fishes in open water also tend to aggregate, a widely recognized defensive behavior in fishes (Eibl-Eibesfeldt, 1962; Hobson, 1968). That aggregating and a quick retreat to cover are adaptive in defense becomes evident when certain open-water predators appear, notably large *Caranx* spp. (Carangidae). In response to this threat, the planktivores assembled to feed above the reefs abruptly close ranks, and then often dive to the reef below.

Despite the convergence among so many unrelated species in features that increase swimming speed, and the obvious adaptive value of these features, certain other planktivorous fishes have accommodated the same threats by taking virtually the opposite evolutionary course. Instead of being more streamlined than their benthic relatives, species of the planktivorous pomacentrid genera *Dascyllus* and *Amblyglyphidodon* are actually deeper-bodied (and have longer fin spines) than benthivorous pomacentrids (Hobson and Chess, 1978). These features retard rather than promote swimming speeds, so if maintaining station in currents and accelerated flight are important, how do these fishes compensate for their reduced swimming efficiency?

They can, of course, avoid strong currents simply by feeding elsewhere, but what about the problem with predators? I suggest that threats from predators are reduced by their greater body depth and spine development, because these features increase the chance of becoming lodged in the mouth or pharynx of predators that would attempt to swallow them. An effective combination of deep bodies and strong fin-spines probably protects benthivorous as well as planktivorous chaetodontids and pomacanthids (Hobson and Chave, 1972). It is significant that the planktivorous species of these two families are, as a group, indistinguishable from their benthivorous relatives on the basis of external morphologies. Many, in fact, are congeners, for example, the planktivorous and benthivorous species of *Chaetodon* (Hobson, 1974).

Clearly, the exceptionally deep bodies characteristic of these predominantly benthivorous families are suited to activities in open water, although perhaps not where strong currents flow. It would seem that while the streamlined bodies and deeply forked caudal fins of many diurnal planktivorous fishes promote eluding predators, the exceptionally deep bodies and long fin-spines of certain others tend to discourage predators. Both combinations may promote access to zooplankton in open water during the day by reducing threats from predators (Fig. 4).

Planktivorous fishes in open water above reefs become increasingly vulnerable with decreasing light, and they respond by moving closer to shelter. Thus, they forage lower in the water column when the sky is overcast than when it is clear, and they descend briefly when clouds pass in front of the sun on otherwise clear days (Hobson, 1972; Stevenson, 1972).

C. Distribution and Movement

Diurnal planktivores are most numerous along reef edges adjacent to deeper water, probably because their major prey—holoplankters from open water (Hobson and Chess, 1978, 1986)—are most accessible there. Consider, for example, their distribution (excluding juveniles) among reef habitats off the island of Hawaii, as determined by visual assessments in belt transects (Hobson, 1974). Diurnal planktivores were of 12 species and constituted 45% of the fishes counted along the drop-off into deeper water, but were only of 6 species constituting 14.6% of the fishes counted over the inner reef.

The abundance of diurnal planktivores near the reef edge comes not only from the many that reside there, but also from others that migrate each morning from nocturnal shelter sites elsewhere on the reef (Hobson, 1972,

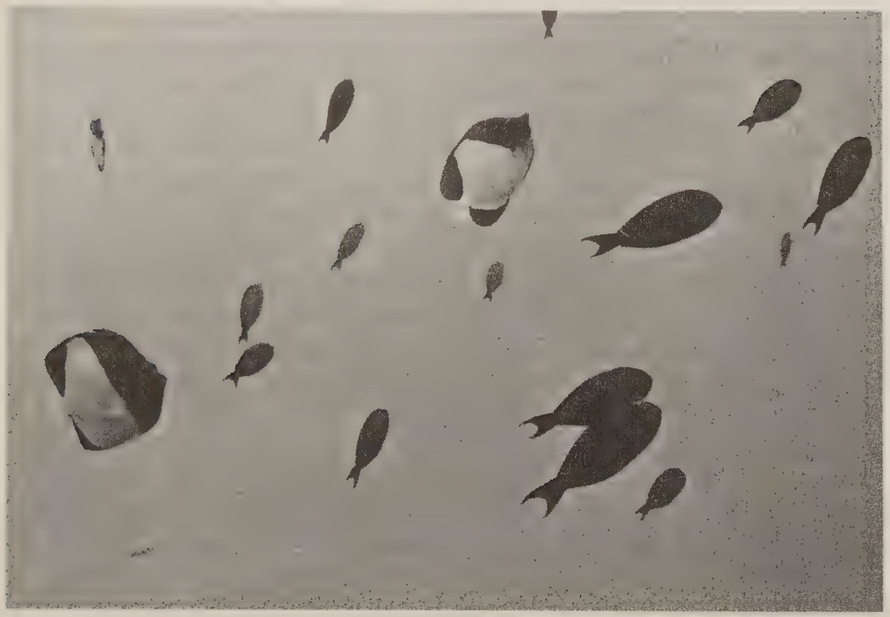

Figure 4 The planktivorous chaetodontid *Hemitaurichthys polylepis* (left) is as deep-bodied as the benthivorous members of its family, whereas the planktivorous acanthurid *Acanthurus thompsoni* (dark fish) is far more streamlined than the benthivorous members of its family.

1973, 1974). Although reef edges tend to be irregular structures rich in shelters used by diurnal planktivores, apparently these shelters cannot accommodate all the planktivores that feed there. That the migrators are among the larger diurnal planktivores (Hobson, 1974) suggests either that there is a shortage of the more spacious shelters at the feeding site or that the smaller species lack the capacity to migrate.

Diurnal planktivores concentrate along the reef edge and feed mainly on transient zooplankters from open water, even though resident zooplankters of comparable type and size are widespread and accessible on many reefs. I refer to the resident zooplankters that occur in dense, generally monospecific swarms close to reef structures, including various copepods (e.g., *Acartia* spp. and *Oithona* spp.) as well as mysids (e.g., *Anisomysis* sp. and *Mysidium* spp.) (Emery, 1968; Hobson and Chess, 1978; Hamner and Carleton, 1979).

These diurnal swarms can be immense. For example, Hamner and Carleton (1979) described a swarm of the copepod *Oithona oculata* encircling a Palauan bay that was more than 100 m long and estimated to contain 75 million individuals. Similarly, Emery (1968) observed among reef formations in the Florida keys swarms of the copepod *Acartia spinata* that ranged in size from just a few to over 60 m^3, with densities of about 110,000 individuals per m^3.

The zooplankters in these swarms, however, seem generally unavailable to predatory fishes. Probably this is because predators confronted with multiple targets have difficulty distinguishing individuals (Welty, 1934; Eibl-Eibesfeldt, 1962; Hobson and Chess, 1978). In concluding that swarms protect their members from predators, Hamner and Carleton (1979, p. 11) noted that planktivores "swim through the swarms as if they were invisible."

Certainly there is some predation on these swarms, just as there is predation on fish schools. For example, Emery (1968) saw predators take copepods from swarms in the tropical Atlantic, and Hobson and Chess (1978) found mysids in the gut contents of diurnal planktivores taken near mysid swarms in the central Pacific. But considering how many individuals there are in these swarms, this predation is probably insignificant. Swarming, therefore, would seem to be an adaptive behavior that reduces the vulnerability of reef zooplankters to reef planktivores.

Because diurnal planktivores feed mainly on transients, they depend on water currents to supply them with food. It is well known that currents are important to feeding planktivores (Stevenson, 1972; Thresher, 1983a), and even casual observations note that there are currents where planktivores are abundant. In fact, it is because their food is transported by currents that planktivorous fishes are able to feed in the stationary aggregations so characteristic of them. As Stevenson (1972) pointed out, the aggregations dissolve when currents slacken and the planktivores are forced to swim about in search of prey. Despite their dependence on currents as transporters of food, however, planktivorous fishes find it increasingly difficult to maintain station when currents exceed optimal velocities (which vary with the species), and ultimately they are forced to shelter (Hobson and Chess, 1976, 1978).

Planktivorous fishes also are distributed relative to their size. Feeding at reef edges, for example, is most characteristic of larger individuals. Thus, species concentrated close to the drop-off (depth about 25 m) into deeper water off the island of Hawaii (Hobson, 1974) are, at sizes exceeding 10 cm SL, the larger of the planktivorous reef fishes there (e.g., the chaetodontids *Chaetodon miliaris* and *Hemitaurichthys polylepis,* the pomacentrid *Chromis verater,* the acanthurids *Acanthurus thompsoni* and *Naso hexacanthus,* and the balistid *Xanthichthys auromarginatus*). The smaller species are more widely distributed. Examples include the pomacentrids *Chromis agilis* and *C. hanui* (combined as *C. leucurus* in that report), which have maximum sizes of about 7 cm SL. Although these two are numerous along the drop-off, they also are abundant above the inner reef, where the larger species are comparatively scarce.

A similar difference in distribution with size exists above the shelf of sand and isolated patch reefs that rims the windward side of the lagoon at Enewetak atoll (Hobson and Chess, 1978, 1986). In that setting, zooplanktivorous fishes of all sizes abound above patch reefs along the shelf's edge (depth about

10 m), but only the smaller subadults and very small species (less than about 6 cm) are numerous above patch reefs on the inner shelf (depth < 5m). [Relatively large herbivorous planktivores are abundant above patch reefs on the inner shelf, where they feed mainly on drifting plant fragments (Hobson and Chess, 1978), but herbivorous planktivores are not considered here because many of their trophic relations are unlike those of zooplanktivorous species.]

Differences in distribution with size can be related to differences in trophic relationships. As noted earlier, the concentration of larger zooplanktivores at the shelf edge is consistent with diets dominated by transient organisms from open water (Hobson and Chess, 1978). The major planktivore above patch reefs along the shelf edge at Enewetak is the adult of *Chromis viridis*, which is larger than most other planktivores at this site even though its maximum size is only about 7 cm SL. [This species was previously known, and identified in that report, as *C. caerulea* (see Randall *et al.*, 1985a).] Tony Chess and I collected 21 of these fish (6.0–7.3, $\bar{X} = 6.5$ cm SL) from above the patch reefs during the day, and of the 1168 zooplankters in their guts, 1047 (89.6%) were 2.5 to 3.0-mm individuals of *Undinula vulgaris*. This calanoid copepod is a major component of the plankton in the Enewetak lagoon, but during the day it is largely absent above the shelf (Gerber and Marshall, 1974; Hobson and Chess, 1986). In fact, the relatively shallow water above shelf patch reefs during daytime is virtually without zooplankters of any kind larger than 1.5 mm (Hobson and Chess, 1986), which probably is why there are so few larger zooplanktivorous fishes there in daylight.

On the other hand, the smaller zooplanktivorous fishes so abundant above patch reefs on the inner shelf at Enewetak during the day find their food readily available. Chess and I collected subadults of three species whose large plankton-feeding aggregations were prominent above the inner-shelf patch reefs: *Chromis viridis* ($n = 13$; 9–40, $\bar{X} = 25.5$ mm SL), *Dascyllus aruanus* ($n = 10$; 16–35, $\bar{X} = 27.5$ mm SL), and *Rhabdamia gracilis* ($n = 20$; 20–36, $\bar{X} = 30.9$ mm SL). None of the varied zooplankters in their guts—mostly crustacea, but also including larvaceans and fish eggs—were larger than 1.0 mm, and plankton collections taken at the time found these smaller forms to be abundant in the water column.

That the larger planktivorous fishes feed mainly on transient zooplankters at the reef's perimeter is particularly evident above reefs swept by currents. Here these fishes concentrate above the upcurrent edge of the reef and are relatively few above the reef downcurrent. Above a southern Californian reef swept by currents that reverse with the tide, for example, Bray (1981) found that larger (>15 cm) individuals of *Chromis punctipinnis* (but not the smaller ones) concentrate to feed on cladocerans, copepods, and larvaceans at whichever end of the reef faces the current, changing ends with each reversal of current.

Furthermore, plankton samples that Bray took both upcurrent and downcurrent of the feeding *C. punctipinnis* showed that these aggregations remove from the inflowing current a significant proportion of the organisms suitable as prey.

A greater availability of suitable prey above upcurrent parts of a reef explains diel movements that I observed in the planktivorous *Clepticus parri* (Labridae) above a reef off St. Croix, U.S. Virgin Islands. From early to mid morning each day, larger individuals (>15 cm) of this species migrated toward the upcurrent end of the reef, and then from mid to late afternoon they returned downcurrent. The similarity of this pattern to the diel migrations that some Hawaiian planktivores make between inner-reef shelter sites and outer-reef feeding grounds (Hobson, 1972, 1973) suggests that the larger *C. parri* found their prey more available upcurrent.

But if prey of the larger planktivores become increasingly scarce in currents that flow over a reef, how is it that prey of the smaller planktivores apparently remain abundant? Part of the answer is that during the day the smaller zooplankters (less than about 1 mm) are vastly more numerous in currents flowing over the reefs. Perhaps a more important reason, however, is that during the day these smaller zooplankters may be relatively safe from reef predators when more than a few meters above the substrate. This is because the predators that threaten them most are themselves relatively small animals that become increasingly vulnerable with distance from shelter in daylight. Smaller planktivorous fishes that feed by day, for example, generally stay within a meter of the reef. And the various mysids and other predaceous crustacea that range into the water column to feed on still smaller zooplankters do so only at night (Hobson and Chess, 1976, 1978). Thus, during the day, smaller zooplankters may enjoy what is in essence a refuge from reef predators in all but the lower levels of currents flowing over a reef. And as the current flows along, individuals from this refuge would be there to replace those of their kind consumed at the lower levels.

D. Trophic Links with Open-Water Communities

It is widely recognized that planktivorous fishes are a major trophic link between coral reef and open-water communities (Emery, 1968; Davis and Birdsong, 1973). Food webs that have been constructed to represent coral reef trophic systems, however, assume that the primary flow of energy from planktivores to other elements of the community is through piscivorous predators (e.g., Polovina, 1984). But while undoubtedly some diurnal reef planktivores are consumed by predators (e.g., Choat, 1968; Hartline *et al.*, 1972), the numbers taken are relatively few owing to effective defenses, as described earlier.

Probably the major path of energy from diurnal reef planktivores to other components of the reef trophic system is through feces. Feeding planktivores produce prodigious amounts of feces that rain down upon the reef throughout the day, and much if not most of this material is consumed by other fishes (Robertson, 1982). Chess and I have found that when zooplankters are especially abundant in the water column, those consumed by planktivores pass through the guts so rapidly that they appear in the feces with little sign of digestion. In this situation the secondary consumers probably gain more energy from the zooplankton than do the planktivores that had consumed them first. Although planktivore feces are most readily ingested by fishes before settling on the seafloor, significant amounts are taken from the bottom by herbivores and detritivores (Robertson, 1982). Most of this coprophagy occurs below the feeding aggregations, but some material still in planktivore guts at day's end is vented at nocturnal shelter sites elsewhere on the reef, and according to Bray *et al.* (1981) this represents a significant importation of energy to the reef benthos.

III. CREPUSCULAR CHANGEOVER

Like virtually all members of the coral reef community, planktivorous reef fishes and their prey find twilight to be a time of transition between distinctive diurnal and nocturnal modes. The changeover process is an orderly complex of responses to specific levels of diminished daylight, with the morning and evening sequences being essentially mirror images of one another (Hobson, 1972; Collette and Talbot, 1972; Helfman, 1986b). Here I describe events during the evening changeover that involve planktivorous fishes and zooplankters.

A. Transition from Day to Night: Fishes

When the diurnal planktivores descend toward the seafloor late in the afternoon they provide the first clear indication that the reef community is shifting toward its nocturnal mode. Although the beginnings of this process cannot be distinguished from the highly variable diurnal condition described earlier by 30 min before sunset it is clear that many diurnal planktivores are descending toward shelter on the reef.

Just as smaller individuals stay closer to the reef while active during the day, they also are the first to shelter in the evening. Consider, for example, the species of *Chromis* in Hawaii (Hobson, 1972): The smallest, *C. vanderbilti* (maximum size about 5 cm SL), stays within a meter or so of the reef on even the brightest days and is dispersed under cover on the reef by 15 min before sunset. The next smallest, *C. agilis* (as *C. leucurus* in that paper; maximum size about 7 cm SL), ranges 1–2 m above the reef during the day and is under cover within a few minutes after sunset. Finally, two larger species of similar size, *C. ovalis* and *C. verater* (maximum size about 14 cm SL), range throughout the water column during the day, and the last of them take cover about 15 min after sunset. The final descent of the larger planktivores marks the beginning of the "quiet period," a 15- to 20-min interval when the waters above the reef appear relatively empty of fishes (Hobson, 1972). It is believed that reef fishes tend to avoid exposed positions at this time because of sharply increased threats from predators. Actually, as the diurnal planktivores demonstrate in descending to cover in order of increasing size, most diurnal fishes have left the water column before the quiet period begins. Apparently the smaller fishes are threatened first—the smallest well before sunset—and after that the danger continues to grow in the fading light, threatening progressively larger fishes, until by the start of the quiet period virtually all diurnal fishes that had been in the water column have been affected. Thus, the timing of the quiet period and other changeover events appears to be determined by levels of light. These events occur earlier under cloudy skies (Collette and Talbot, 1972) and are extended in the longer twilight at higher latitudes (Helfman, 1981, 1986b; Hobson, 1986).

The nocturnal planktivores enter the waters above the reef at nightfall in the same order by size that the diurnal species leave—smaller ones first. The smallest appear while some of the diurnal species still hover low in the water column, well before the quiet period has begun. The first of them are less than 3 cm in size and not readily visible (many are highly transparent). Among the first to rise above the reef are juvenile *Apogon* spp. (Apogonidae), which are prominent members of tropical reef communities worldwide. A previous discussion of the early appearance of largely transparent juvenile apogonids (Hobson *et al.*, 1981, p. 23) stated:

> This entry into exposed locations when many piscivorous predators hunt most effectively might seem in conflict with the quiet period concept. But in the dim light we are not surprised that these inconspicuous little fish seem to go unseen by the visual hunters that so seriously threaten the more visible adults. Certainly these juveniles go unseen by human eyes at this time, except under close inspection with a diving light, and so fail to detract from the aura of inactivity that characterizes the quiet period.

On many tropical reefs the quiet period comes to an abrupt end about 30 min after sunset, when hordes of *Myripristis* spp. (Holocentridae) surge into the water column from their daytime shelters in the reef (Hobson, 1972) (Fig. 5A and B). Other planktivorous fishes follow in short order, including *Priacanthus* spp. (Priacanthidae). As is the case among their diurnal counter-

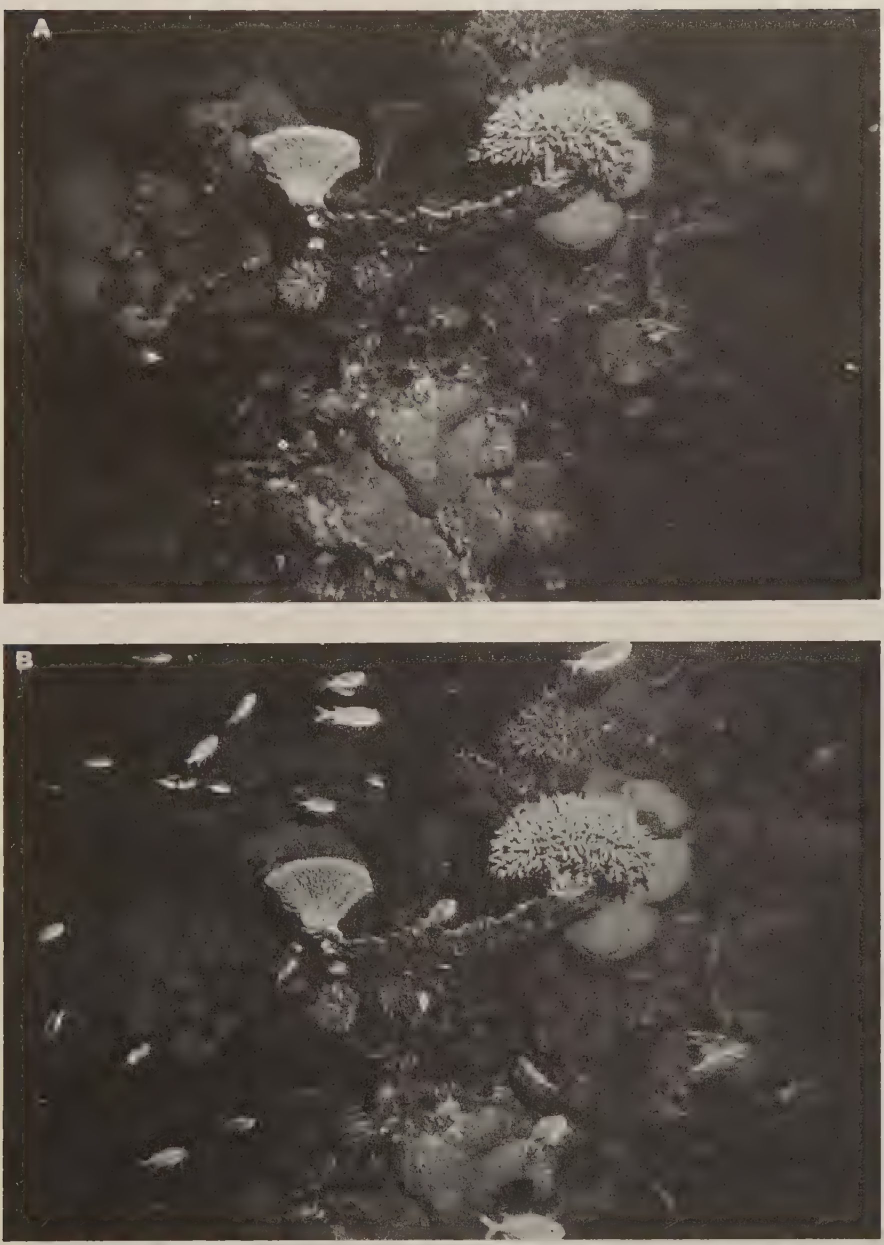

Figure 5 A reef in the lagoon at Enewetak Atoll (A) 30 min after sunset and (B) 2 min later, as numerous *Myripristis* spp. emerge from shelter.

parts, while most nocturnal planktivores forage above their diurnal refuges, some migrate to more distant feeding grounds (Hobson, 1973). Among the migrators are *Myripristis murdjan*, *M. amaena*, and *Priacanthus cruentatus*, which head seaward in groups after emerging from Hawaiian reefs about 35 min after sunset (Gosline, 1965; Hobson, 1972). Other migrators include *Pempheris schomburgki* in the tropical Atlantic. After emerging from shelters along the inside of a Virgin Island reef at nightfall, members of this species swim in schools close to the coral as they cross the reef to nocturnal feeding grounds in the water column outside (Gladfelter, 1979) (Fig. 6).

B. Transition from Day to Night: Zooplankters

Transient zooplankters of types consumed by diurnal planktivores greatly increase in size and number above shallow-water reefs after dark. At Enewetak Atoll, for example, the major prey of diurnal planktivores—calanoids of 1–3 mm—increased more than fivefold in numbers above reefs on the lagoon shelf during the two hours immediately after sunset. During the day these calanoids were abundant as prey of reef planktivores only at the shelf's edge and

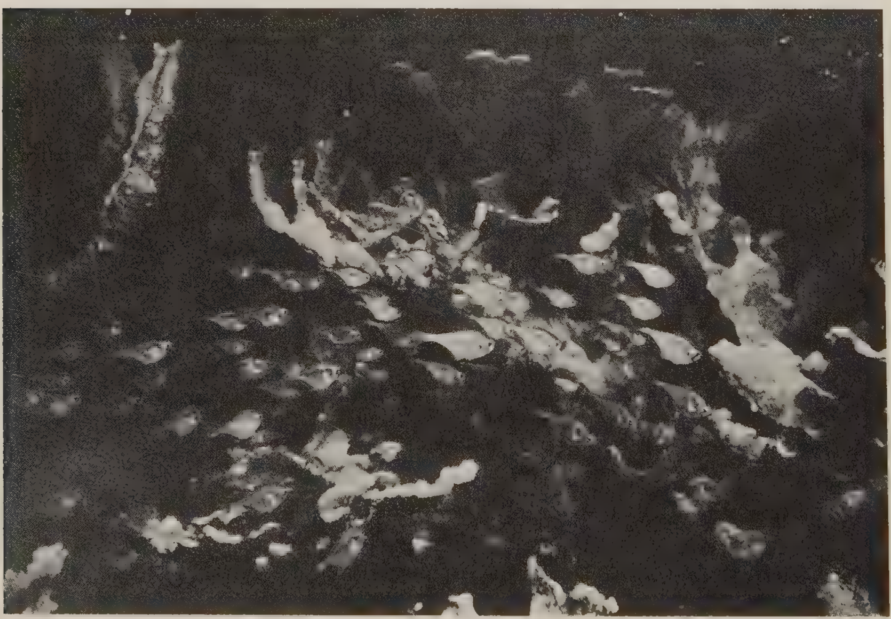

Figure 6 A school of *Pempheris schomburgki* (Pempheridae) following its crepuscular migration route to feeding grounds along the seaward side of a reef at St. Croix, U.S. Virgin Islands. Silvery specks at upper right are atherinids that have dispersed from diurnal schools among the coral for nocturnal feeding above the reef.

in water that had flowed through the deeper passes from the open sea (except for individuals trapped in shallow water at sunrise, as detailed in the following). But beginning during late twilight, calanoids of this size were among the many forms that became increasingly numerous in the waters above the shelf. It was obvious that they had arrived in currents that flowed over the interisland reefs from the open sea outside the atoll—currents that carried relatively few such forms during the day. Considering that Enewetak is in the path of the trade winds and the oceanic Equatorial Current, it seems probable that the increased numbers of zooplankters in water flowing over the interisland reef at night include organisms that shortly before had risen to the surface from ocean depths windward and upcurrent of the atoll (Hobson and Chess, 1986).

A rich assortment of reef residents join the open-water transients above reefs late during the changeover. They include the holoplankters that had been in swarms close to benthic substrata during the day, mostly copepods and mysids (Emery, 1968; Hobson and Chess, 1978; Hamner and Carleton, 1979), but that at nightfall disperse throughout the water column. Even more prominent, however, are a variety of semipelagic organisms that enter the water column during the night from positions in or on the seafloor. Many of these are primarily benthic organisms that spend only a relatively short period of time in the water column. They include various polychaetes, ostracods, copepods, mysids, isopods, amphipods, and crustacean larvae (Alldredge and King, 1977, 1980; Robichaux *et al.,* 1981; McWilliam *et al.,* 1981). The residents vary widely in size, from well under 1 mm to more than 10 mm, and generally include the largest of the zooplankters above reefs at night (Hobson and Chess, 1978, 1986).

IV. NOCTURNAL PLANKTIVORES

The fishes that forage on zooplankters above tropical reefs at night have been strongly influenced by the difficulty of visually locating prey in dim light, as evidenced by the exceptionally large eyes of *Myripristis* spp. (Fig. 7). The differences in morphology and behavior between nocturnal planktivores and their diurnal counterparts shows that selection pressures affecting planktivore form and function differ greatly between day and night.

A. Adaptations to a Nocturnal Planktivorous Diet

The major prey of most nocturnal reef planktivores are among the relatively large (>2 mm), semipelagic residents of the local habitat that rise into the water column at some time during the night (Hobson, 1974; Hobson and Chess, 1978; Gladfelter, 1979). Other important prey are larger holoplankto-

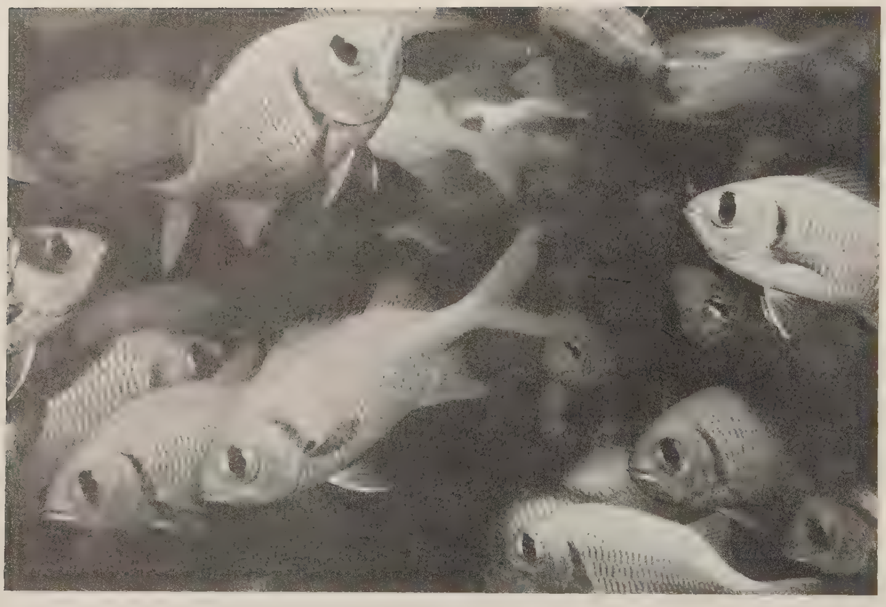

Figure 7 An aggregation of the nocturnal planktivore *Myripristis amaenus* (Holocentridae) in a Hawaiian reef cave during the day.

nic residents, such as mysids, and still others are larger transients from open water, like euphausids (Hobson and Chess, 1978). Conspicuously absent from this diet, however, are the relatively small transient holoplankters that are major prey of the diurnal planktivores, even though these organisms are more abundant at night than during the day (Hobson and Chess, 1978, 1986).

One might take these findings as evidence that nocturnal planktivores make a choice based on preference for larger prey, citing the widespread belief that planktivorous fishes choose the largest organisms available to them (Zaret, 1980). A corollary to this belief is that incentive to take the smaller zooplankters is lost in the presence of larger alternatives, which is consistent with the observation that natural selection for abilities to consume smaller prey is much reduced at night. (Consider, for example, that nocturnal planktivores generally lack the highly evolved modifications of head and jaws that enable even the larger diurnal planktivores to consume tiny prey in open water.) But despite compelling arguments that support this reasoning, I believe larger zooplankters are taken at night, not because they are preferred or that it is more efficient to do so, but rather because they simply are more vulnerable.

That nocturnal planktivores feed mainly on the larger components of the plankton may have less to do with preference for larger prey than with inability to see the smaller ones. Studies that have shown preference for larger prey have been done in daylight (e.g., Brooks and Dotson, 1965; Coates, 1980) and so fail to consider how lack of light would influence what is available to planktivorous fishes at night. Most nearshore fishes that use vision to feed at night have sacrificed visual acuity for visual sensitivity, which limits their ability to see smaller objects (Walls, 1967; Munz and McFarland, 1973). The greatly enlarged eyes of *Myripristis* spp. and *Priacanthus* spp., for example, permit these fishes to sense visual cues in the nocturnal water column, but apparently these cues do not include the smaller zooplankters. This limitation readily accounts for the observed lack of selection for features that permit a diet of smaller prey, noted earlier, because obviously predators that feed by sight would have little use for trophic mechanisms that accommodate prey too small for them to see.

An inability to see the smaller zooplankters would also explain why my studies with Chess have found that generally even the smallest nocturnal reef planktivores are limited to zooplankters larger than about 1 mm, even where comparably sized diurnal planktivores feed primarily on organisms smaller than this. One might attribute this to the smaller mouths generally found in "comparably sized diurnal planktivores," but our studies have shown that nocturnal planktivores feed on larger prey even when they have feeding structures similar to those of their diurnal counterparts.

Consider, for example, the juveniles of two closely related apogonid species, *Apogon cyanosoma* and *Rhabdamia gracilis* [considered congeners by Lachner (1953), with *A. cyanosoma* as *A. novae-guineae*]. Despite similar feeding mechanisms (both have the generalized trophic features of basal percoids), the juveniles of *A. cyanosoma* feed at night and consistently take larger zooplankters, whereas the juveniles of *R. gracilis* feed by day and consistently take smaller zooplankters. This finding is based on data from specimens that Chess and I collected above a patch reef on the lagoon shelf at Enewetak during one night and the following day. Here, the 45 calanoid copepods in the guts of five nocturnal *A. cyanosoma* (20–27, $\overline{X}$ = 23.6, mm SL) were 2 to 3 mm in size, whereas the 70 calanoids in the guts of five diurnal *R. gracilis* (17–37, $\overline{X}$ = 27, mm SL) were 0.3 to 2 mm. Clearly this difference in size of prey, day compared to night, was determined by something other than size of mouth in these morphologically similar predators.

The absence of larger copepods in the diet of the diurnal *R. gracilis* is readily explained by the scarcity of these prey in the daytime water column above the shelf, as noted earlier. But similar reasoning cannot account for the absence of smaller copepods in the diet of the nocturnal *A. cyanosoma* because these are so abundant at night—far more numerous than the larger ones, in fact. Although it is possible that the smaller zooplankters were simply ignored when the larger ones became available at night, I would expect the juvenile *A. cyanosoma* to have taken at least some of them if they could, and the fact that they did not seems best explained by visual limitations.

I know of one nocturnal planktivore that feeds regularly on zooplankters smaller than 1 mm, but this exception to the generalization can be explained. *Praneseus pinguis* (Atherinidae), which is peripherally associated with reefs in the lagoons of western Pacific atolls, feeds heavily on organisms as small as 0.2 mm during nighttime excursions from nearshore schooling sites to offshore feeding grounds. But this fish feeds right at the water's surface, where submarine starlight and moonlight are strongest (Hobson and Chess, 1973), so its visual capabilities likely differ from those of species adapted to dimmer light at greater depths.

Presumably factors other than size contribute to the relative vulnerability of various zooplankters at night. Many of the semipelagic residents, in particular, are more opaque than the more numerous holoplankters among which they occur after dark, and these are appropriate targets in dim light. Others are awkward swimmers, for example, caprellid amphipods, and therefore are less elusive and also more likely to create the turbulence and resulting bioluminescence thought to direct many nocturnal attacks (Hobson *et al.*, 1981).

That nocturnal planktivores have generalized feeding mechanisms does not mean they lack specialized trophic features. The mouths of some resemble the mouths of diurnal planktivores in being sharply upturned (Fig. 7), so obviously the advantage of this arrangement, noted earlier for diurnal species, has adaptive value among nocturnal planktivores as well. I have mentioned the exceptionally large eyes of many, which certainly are highly specialized means to orient visually in dim light and presumably to locate prey. Significantly, eyes of species active at middle depths tend to be larger than eyes of species active at the base of the water column, probably because the light available close to the seafloor is increased by reflected moonlight and starlight (Hobson *et al.*, 1981).

B. Adaptations to Nocturnal Threats from Predators

There is morphological and behavioral evidence that threats from predators are significantly reduced at night. For example, the streamlined bodies and deeply forked caudal fins so widespread among diurnal planktivores are much less developed among their nocturnal counterparts. So if these features are adaptive in providing the speed needed to evade attacks, as suggested earlier, their general absence among the nocturnal species could mean there is less threat of attack after dark (Hobson, 1973, 1979).

Similarly, the tendency to aggregate while feeding in the water column, which is thought to be a defense against predators (Eibl-Eibesfeldt, 1962) and is so strong by day, is much weaker at night. Some, including various *Myripristis* spp., are active in loose aggregations, especially in moonlight, but many others, including various *Apogon* spp., are solitary (Hobson, 1968, 1974). Some individuals of *Priacanthus cruentatus* school high in the water column as they migrate seaward shortly after nightfall, but other individuals of this species are solitary as they remain above the reef during the night (Hobson, 1974).

Even those nocturnal planktivores commonly described as "schooling fishes" based on their daytime assemblages, for example, various clupeids and atherinids (Randall, 1967), generally disperse at night in favor of independent activity and small, loosely associated feeding groups (Starck and Davis, 1966; Hobson, 1968). So if aggregations are adaptive by reducing the threat of attack, the nocturnal condition would indicate relative freedom from such threats.

Certainly the visually directed attacks that threaten smaller fishes during the day would be limited by the sharp decrease in ambient light at night. Nevertheless, it would seem that at least some of the reduced nocturnal threat comes from conventional attackers. Examples include *Caranx marginatus* and *Selar crumenophthalmus* (Carangidae), which hunt smaller fishes at night in the Gulf of California (Hobson, 1968). These two species have morphologies typical of aggressive, open-water predators, but with large eyes that may allow them to attack in the ordinary way using the much lower levels of ambient light produced by moon and stars. Support for this possibility comes not only from the tendency of nocturnal planktivores like *Myripristis* spp. to aggregate under moonlight, but also from the countershaded nocturnal coloration of *Myripristis* spp., that is, dark above and light below (Hobson, 1968). If Longley (1917) and others are correct that such countershading effectively conceals midwater fishes from predators, this feature in nocturnal planktivores would suggest that they are threatened by predators that use light from above—presumably moonlight or starlight—to direct their nocturnal attacks.

The major visual cues above coral reefs on darker nights or in deeper water, however, probably are the emissions of luminescent organisms, which must have profound effects on nocturnal interactions between predators and prey (Hobson, 1966; Hobson *et al.,* 1981). Certainly the straightforward charge typical of predators that threaten diurnal planktivores would be less effective amid luminescent organisms on dark nights. Because luminescence among the plankton is greatly increased around moving objects, an aggressive charge by a large predator would be advertised as soon as launched, giving prey time for evasive maneuvers. Furthermore, while a charging predator could target on luminescence around its prey, I question whether this tactic would be successful if the attack is launched from some distance away. This is because the luminescent organisms that elicited the attack would be left behind as the fish darts away, thus leading the attacker to the wake of the fleeing fish (Hobson *et al.,* 1981). On the other hand, nocturnal piscivores may attack the leading edge of the luminescent trail.

But even if nocturnal planktivores are relatively free of attacks like those that threaten diurnal species, they may be threatened by some other type of predator in situations where defenses effective in daylight are irrelevant (Hobson, 1973). A predator that is effective amid luminescent organisms at night might be one that hovers motionless, waiting for prey to betray themselves by movement that produces turbulence and resulting luminescence. This tactic would be in essence an ambush, and effective only at short range. Although the predator could be led by luminescence to prey some distance away, probably its approach must involve great stealth to avoid turbulence and resulting bioluminescence (Hobson *et al.,* 1981). In this regard, one might consider the carangid *Selene brevoorti*, a predator that feeds on smaller fishes at night in the Gulf of California (Hobson, 1968). The extraordinary morphology of this species suggests unusual feeding behavior; in fact, its deep body, laterally compressed to an extreme, might well prove adaptive in maneuvering with minimum turbulence to approach unseen close to prey in the dark.

C. Distribution and Movement

Nocturnal planktivores generally are more widespread throughout the reef area than are their diurnal counterparts. Presumably this distinction has developed because the nocturnal species feed mainly on reef residents that are themselves widespread over the reef, whereas the diurnal species take mainly open-water transients that are most available at reef edges. In addition, a decreased threat of predation at night is evident in the tendency of the nocturnal species to disperse, at least during moonless nights, while the diurnal species tend to cluster.

Although most nocturnal planktivores feed near their shelter sites, many migrate to feeding grounds elsewhere—much as do certain diurnal planktivores. Some of the migrators go to other parts of their home reef, where they nevertheless continue to feed mainly on semipelagic reef residents, apparently they find them more abundant in these other places. An example is *Pempheris schomburgki,* which migrates during twilight from shelters along the inside of a Virgin Island reef to feeding grounds along the outside (Gladfelter, 1979). Other migrators that apparently go to the edge of the reef or beyond and feed on open-water transients. For example, while some individuals of *Priacanthus cruentatus* remain to feed in the local area after emerging from Hawaiian reefs, many others migrate seaward; and when they return, about 40 min before sunrise, their stomachs are full of pelagic organisms, including cephalopods and crab megalopae (Gosline, 1965; Hobson, 1972, 1974).

Nocturnal and diurnal planktivores tend to differ in their distributions relative to the effects of water currents on availabilities of their major prey—resident and transient zooplankters, respectively. The nocturnal planktivores are less numerous in stronger currents, perhaps because their resident prey tend to avoid currents that would carry them from their home grounds. The diurnal planktivores, on the other hand, concentrate in currents that carry their transient prey from deeper water (Hobson and Chess, 1978, 1986). This is not to say that nocturnal planktivores always avoid currents, or that diurnal planktivores always are attracted to currents. To the contrary, nocturnal planktivores often feed to advantage in currents that can be tolerated by their resident prey (Thresher, 1983a), and diurnal planktivores avoid currents that exceed velocities in which they themselves can maintain station (Hobson and Chess, 1978).

Furthermore, stronger currents from deeper water should benefit nocturnal planktivores that prey heavily on larger transient zooplankters that appear above reefs after dark, as does *Myripristis pralina* at Enewetak (Hobson and Chess, 1978). Similarly, if the seaward twilight migrations of *Myripristis murdjan, M. amaenus,* and *P. cruentatus* in Hawaii are headed for feeding grounds above the outer drop-off, as surmised (Hobson, 1972, 1974), then they too would benefit from currents strong enough to supply them with zooplankters from the open sea.

Many nocturnal planktivores have distinctive defensive needs that affect their distributions during diurnal periods of rest. Unlike the diurnal planktivores, which generally are solitary while at rest during the night, many nocturnal planktivores are highly gregarious in their daytime resting mode. This is particularly evident in the clupeids, engraulids, and atherinids that shelter in dense, inactive schools close to reefs during the day. Examples from the tropical Atlantic include *Jenkinsia lamprotaenia* (Clupeidae) and *Allanetta harringtonensis* (Atherinidae), which school among reef structures by day and disperse to feed above the reef at night (Starck and Davis, 1966). Other nocturnal planktivores, more secretive than the schoolers, aggregate by day deep in the shadows of reef caves and crevices. These include *Myripristis* spp. in Hawaii (Hobson, 1972, 1974) and *Pempheris schomburgki* in the Virgin Islands (Gladfelter, 1979).

D. Trophic Links with Open-Water Communities

Nocturnal planktivores that feed mainly on resident zooplankters do not represent direct trophic connections with open-water communities, as do most diurnal planktivores. They are, of course, intermediate links in the transfer of energy between the two realms because so many of their resident prey consume oceanic materials. Their importance in this role, however, is diluted by the many other predators that consume these same prey close to the reef. On the other hand, those nocturnal planktivores that feed on transient zooplankters from the open sea do represent direct trophic connections with the oceanic realm.

The subsequent flow of energy from nocturnal planktivores to other elements of coral reef communities goes primarily through piscivorous predators, which, as noted earlier, probably is not true of diurnal planktivores. In contrast to the diurnal species, which seem relatively secure from predators, many of the nocturnal planktivores are primary prey—particularly the schooling clupeids and atherinids (Randall, 1967; Hobson, 1968). These fishes are most vulnerable to predators not while active in the water column at night, or even while at rest in schools during the day, but rather during the crepuscular transition between these conditions (Hobson, 1968).

It seems unlikely that feces of nocturnal planktivores can compare with feces of diurnal planktivores as transporters of energy to other elements of the community. Two problems limit the effectiveness of nocturnal coprophagy among fishes: first, the feces are more difficult to see in the dim light of night and, second, the more dispersed nocturnal planktivores do not offer the focal points of activity that greatly facilitate coprophagy by day. Furthermore, because the nocturnal planktivores take larger and fewer prey, digestion is slower and evacuation less frequent.

Thus, the continuous rain of feces beneath aggregations of diurnal planktivores that makes coprophagy such a viable feeding mode during the day is unlikely to be duplicated at night. Still, feces that settle on the reef beneath nocturnal planktivores, at either feeding sites or resting places, are likely to enter the coral reef food chain through vertebrate or invertebrate detritivores. One study found exceptional growth among corals at the daytime resting places of juvenile grunts (Haemulidae), which are nocturnal planktivores, and attributed this to nourishment from the excretory and fecal products of these fishes (Meyer *et al.,* 1983).

V. VULNERABILITY OF ZOOPLANKTERS ABOVE REEFS

It is clear that zooplankters of more than about 1 mm in size are highly vulnerable to planktivorous fishes when in the water column above coral reefs during the day. Most that experience this vulnerability are of open-water species and have encountered the reef habitat by chance. There are few reef residents among them because most of these shelter by day in swarms or under benthic cover. That this sheltering behavior is adaptive as a defense is evident in the intensity of predation suffered by transients that come within reach of reef planktivores.

Zooplankters are less vulnerable above coral reefs at night, as evidenced by the great numbers of them there during that period. The nocturnal increase involves reef residents that had abandoned their daytime shelters and also open-water transients that had arrived in the reeftop flow after upcurrent populations made their nightly ascent into the surface waters. Those taken by nocturnal planktivores tend to be relatively large, opaque forms that are unavailable by day; the far more abundant smaller forms so heavily exploited by diurnal planktivores are relatively unimportant as prey of nocturnal planktivores despite their greatly increased numbers above the reef after dark. It would appear that vulnerability to nocturnal planktivorous fishes involves features visible in dim light.

That zooplankters above reefs are more generally vulnerable in daylight is reaffirmed at dawn. At this time, reef residents that had been dispersed in the water column during the night rejoin swarms or return to benthic shelter, while open-water transients are left exposed to the developing threat from diurnal planktivores. Although the number of transients arriving in the reef-top flow had dropped sharply after upcurrent populations made their regular predawn descent into the depths, many that had been carried above the reef during the night are still there at daybreak and these become vulnerable to diurnal planktivores (Hobson and Chess, 1986). The problem of transients from the open sea trapped in relatively shallow water at daybreak is one widely experienced by zooplankters that make diel vertical migrations in deep water close to reefs, shelves or banks. Reports have cited occurrences above continental shelves (e.g., Issacs and Schwartzlose, 1965; Pereyra *et al.,* 1969) and at the edge of submarine canyons (Chess *et al.,* 1988).

The vulnerability of open-water zooplankters trapped by a relatively shallow sea bed at daybreak exaggerates the more widespread vulnerability of transients that experience incidental contact with reef habitats during the day. These are problems of organisms lacking an effective defense in situations outside their evolutionary experience. Clearly they are a rich and vulnerable source of food for reef fishes, as demonstrated by the range of specialized features these fishes have acquired to exploit them.

I suggest, therefore, that it is the vulnerability of organisms in unfamiliar surroundings that accounts for most planktivory among fishes above coral reefs, at least during the day. It should be expected that zooplankters adapted to the pelagic environment would be vulnerable to predators in reef habitats because they are unlikely to have defenses specific to that setting. Their encounters with reefs must be exceptional events and features that would adapt them for this experience are likely to be maladaptive in their normal open-water habitat.

VI. TOPICS FOR FURTHER STUDY

Certain key features of topics considered in this chapter call for further study, for example:

1. We need more data on the distribution of planktivorous fishes and zooplankters relative to size. I have described the larger planktivorous

fishes concentrated at reef edges, with smaller species and subadults more widely distributed over inner reefs, and attributed this to the pattern of availability of zooplankters of different sizes. This assessment is based on widespread observations, sampling, and impressions, but more data are needed. Confirmation calls for extensive censusing of the planktivorous fishes with concurrent sampling of the plankton, both with emphasis on distribution by size.

2. It is clear that currents are important in the trophic dynamics between fishes and zooplankters, but we need to refine our knowledge of the relationships involved. I have noted that diurnal planktivores tend to concentrate in currents because these carry their transient prey, whereas nocturnal planktivores tend to concentrate away from stronger currents because these are avoided by their resident prey. But there are many exceptions to these generalizations that should be thoroughly analyzed because they provide insight into the relationships involved. For example, one might consider circumstances where nocturnal planktivores feed on transient zooplankters in currents, or on resident zooplankters in relatively weak or intermittent currents.
3. Judgments on adaptive significance generally are based heavily on inference, and they call for further study. For example, I have suggested that streamlining is adaptive both in accelerating flight to shelter and in maintaining station in current. With one complementing the other, the two could be an exceptionally powerful evolutionary force. Whether either or both are active in a specific instance may be evident in the extent of streamlining in planktivores exposed to the prevailing current, especially if there is a concurrent measure of relative danger from predators. The same analysis would provide some basis for accepting or rejecting my suggestion that an exceptionally deep body and strong fin spines allow some fishes to feed in the water column with an acceptable degree of safety. These species would not of course be expected where there is need to maintain station in a strong current.
4. The role of trophic interactions among reef fishes and zooplankters in transferring energy from open water to the reef community is a rich area for study. This chapter identifies major routes involving predation and coprophagy, but the energetics at each link remain to be quantified.
5. What is the nature of nocturnal threats to planktivorous fishes? Nocturnal planktivores lack certain morphological and behavioral features thought to protect their diurnal counterparts from predators, and I have noted this as evidence that threats from predators are reduced at night. It is possible, however, that nocturnal planktivores simply have no use for these defenses because they face different kinds of threats.

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Composition of the Incidental Kill of Small Cetaceans in the US Purse-Seine Fishery for Tuna in the Eastern Tropical Pacific During 1989

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ABSTRACT

The composition of the 1989 incidental kill of small cetaceans during 123 fishing trips by the US tuna purse-seine fleet is given by area, species, stock, sex, length, and, for females, reproductive condition. This year was the first of three consecutive years (1989-1991) in which 100% of the fishing trips will be observed. Mortality was reported for spotted dolphins from the northern offshore and southern stocks, spinner dolphins from the eastern stock and northern and southern whitebelly stocks, common, striped, bottlenose and rough-toothed dolphins and a short-finned pilot whale. The number of females from which reproductive samples were collected and for which species/stock was known increased from 767 in 1988 to 1,323 in 1989.

INTRODUCTION

Dolphins have been taken incidentally in the yellowfin tuna purse-seine fishery in the eastern tropical Pacific Ocean (ETP) since 1959. National Marine Fisheries Service (NMFS) biological technicians have observed at least some of the fishing trips on US vessels since 1968 for the collection of data on mortality, stock identity and life history and have done so in a systematic manner for estimates of fishing mortality since 1975 (Lo *et al.*, 1982). In January 1979, the Inter-American Tropical Tuna Commission (IATTC) began a complementary program on US and non-US vessels and has reported on the total mortality of dolphins in recent years (Hall and Boyer, 1986; 1987; 1988; 1989; 1990).

The composition of the observed kill of dolphins has been reported to the IWC by the NMFS since 1979 (Perrin and Oliver, 1982; Oliver *et al.*, 1983; Wahlen *et al.*, 1986; 1987; 1988; Chivers *et al.*, 1989; 1990). The dolphin species primarily taken are spotted dolphins (*Stenella attenuata*), spinner dolphins (*S. longirostris*) and common dolphins (*Delphinus delphis*), while several other species are taken in low numbers. This report documents the composition of the observed kill on US-registered vessels during 1989.

METHODS

Data were collected by IATTC and NMFS biological technicians (observers) aboard US-registered tuna purse-seine vessels in the ETP. In previous years, only a sample of the vessels carried observers (Lo *et al.*, 1982) except for 1987 when virtually all fishing trips on US vessels were observed. In 1989, a 3-year program of 100% observer coverage began. However, three 1989 trips were not observed in their entirety. These trips departed in late 1988 and were not initially scheduled to carry observers. Observers were placed on these vessels between 4–21 January 1989. Only 44 of 6,708 fleet days (0.01%) were not observed during 1989.

The observers collect an extensive set of data on the location, date, time and circumstances of each set as well as information on the school of dolphins. The number of dolphins killed during a set in which mortality occurred is tallied with, when possible, data on the stock, sex and, for spotted dolphins, relative age (colour phase). A subset of the animals killed is brought on board the tuna vessel making them available for the collection of life-history data and samples. The procedures for collection of life-history data have been described by Perrin *et al.* (1976). Samples of data-collection forms are given in Perrin and Oliver (1982), although the life-history form has changed since that report (Fig.1).

The number of small cetaceans observed killed has been summarised by geographic area, species, sex and length as in previous years' reports and described by Henderson *et al.* (1980). Reproductive condition for females has been summarised by species. For spotted and spinner dolphins, data on kill and reproductive condition have also been stratified by stock using the stock designations of Perrin *et al.* (1985).

RESULTS

There were 123 trips on US-registered tuna purse-seine vessels fishing in the ETP during 1989, 106 of which reported dolphin kill. These trips resulted in an observed kill of 12,548 small cetaceans. The geographic distribution of purse-seine sets with kill observed is shown by 5° block (Fig. 2) and by species/stock and sex, when available (Tables 1–2).

Life-history data were collected on 90 trips. Data were collected from spotted, spinner, common, striped (*S. coeruleoalba*), and bottlenose (*Tursiops truncatus*) dolphins. This represented a sample of 1,756 females for which length data and/or reproductive samples were collected and 1,384 males for which length was collected, excluding 44 spinner dolphins for which stock was unidentified (Tables 3 and 4). No life-history data were collected from 13 rough-toothed dolphins (*Steno attenuata*) or one pilot whale (*Globicephala macrorhynchus*) observed killed. No reproductive data or samples were collected from striped or bottlenose dolphins.

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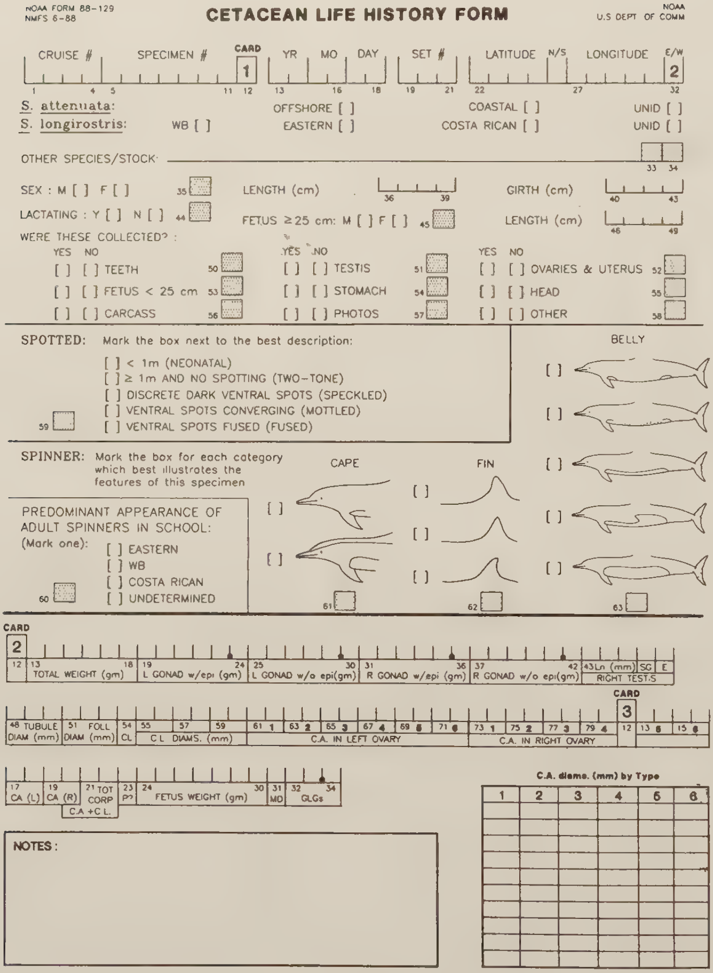

NOAA FORM 88-129
NMFS 6-88

CETACEAN LIFE HISTORY FORM

NOAA
U.S DEPT OF COMM

CRUISE # (1–4) SPECIMEN # (5–11) CARD 1 (12) YR (13) MO (16) DAY (18) SET # (19–21) LATITUDE N/S (22) LONGITUDE (27) E/W 2 (32)

S. attenuata: OFFSHORE [ ] COASTAL [ ] UNID [ ]
S. longirostris: WB [ ] EASTERN [ ] COSTA RICAN [ ] UNID [ ]

OTHER SPECIES/STOCK: ____ 33 34

SEX : M [ ] F [ ] 35 ☐ LENGTH (cm) 36–39 GIRTH (cm) 40–43
LACTATING : Y [ ] N [ ] 44 ☐ FETUS ≥25 cm: M [ ] F [ ] 45 ☐ LENGTH (cm) 46–49

WERE THESE COLLECTED? :

YES NO			YES NO			YES NO	
[ ] [ ] TEETH	50 ☐		[ ] [ ] TESTIS	51 ☐		[ ] [ ] OVARIES & UTERUS	52 ☐
[ ] [ ] FETUS < 25 cm	53 ☐		[ ] [ ] STOMACH	54 ☐		[ ] [ ] HEAD	55 ☐
[ ] [ ] CARCASS	56 ☐		[ ] [ ] PHOTOS	57 ☐		[ ] [ ] OTHER	58 ☐

SPOTTED: Mark the box next to the best description:

[ ] < 1m (NEONATAL)
[ ] ≥ 1m AND NO SPOTTING (TWO-TONE)
[ ] DISCRETE DARK VENTRAL SPOTS (SPECKLED)
[ ] VENTRAL SPOTS CONVERGING (MOTTLED)
59 ☐ [ ] VENTRAL SPOTS FUSED (FUSED)

BELLY
[ ]
[ ]
[ ]
[ ]
[ ]
63 ☐

SPINNER: Mark the box for each category which best illustrates the features of this specimen

CAPE
[ ]
[ ]
61 ☐

FIN
[ ]
[ ]
[ ]
62 ☐

PREDOMINANT APPEARANCE OF ADULT SPINNERS IN SCHOOL: (Mark one):
[ ] EASTERN
[ ] WB
[ ] COSTA RICAN
60 ☐ [ ] UNDETERMINED

CARD 2

12	13–18	19–24	25–30	31–36	37–42	43		
2	TOTAL WEIGHT (gm)	L GONAD w/epi (gm)	L GONAD w/o epi(gm)	R GONAD w/epi (gm)	R GONAD w/o epi(gm)	Ln (mm)	SG	E
						RIGHT TESTIS		

48	51	54	55	57	59	61 1	63 2	65 3	67 4	69 5	71 6	73 1	75 2	77 3	79 4	CARD 3 12	13 5	15 6
TUBULE DIAM (mm)	FOLL DIAM (mm)	CL	C L DIAMS. (mm)			C.A. IN LEFT OVARY						C.A. IN RIGHT OVARY				3		

17	19	21	23	24–30	31	32–34
CA (L)	CA (R)	TOT CORP	P?	FETUS WEIGHT (gm)	MO	GLGs
	C.A +C L.					

NOTES :

C.A. diams. (mm) by Type

1	2	3	4	5	6

Fig.1. Current version of the cetacean life-history form.

DISCUSSION

Data on the level of incidental mortality and biology of dolphins taken by the tuna purse-seine fleet in the ETP have been collected since 1968. In only one year prior to 1989, in 1987, have virtually all fishing trips been observed (in 1987, 123 of 134 trips and 95% of fleet days were observed). A relatively low level of biological sampling occurred during most of the 1980s. This level increased during 1987 (from 370 sets of reproductive samples from females for which species/stock was known in 1986 to 912 in 1987). The sampling rate (proportion of observed kill from which samples were collected) in 1987 increased slightly during 1988, from 6% to 7%, but because only 50% of the fishing trips were observed in 1988, fewer samples were collected (n=767). In 1989, the sampling rate increased to 11% and the number of reproductive samples collected increased to 1,323 from females of all species for which species/stock was known.

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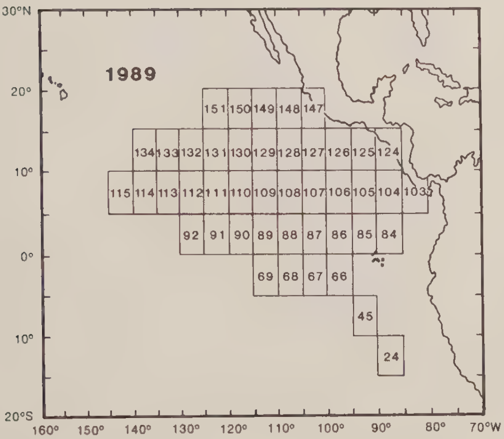

Fig.2. Geographic distribution of the observed incidental kill of dolphins during 1989 on US-registered vessels by 5° block. The numbered blocks without shading are regions where incidental kill was observed but no life-history data were collected. The shaded blocks show those regions where life-history data as well as mortality data, were collected.

Table 1

Total kill of spotted and spinner dolphins by stock, sex (M = male, F = female) and 5° square (see Fig.2 for location of blocks). No kill was reported for coastal spotted dolphins. 263 spinner dolphins not identified to stock were excluded from the table.

	Spotted dolphins						Spinner dolphins								
	Northern offshore			Southern offshore			Eastern			Northern whitebelly			Southern whitebelly		
5° block	M	F	Total	M	F	Total	M	F	Total	M	F	Total	M	F	Total
24	0	0	0	1	0	1	0	0	0	0	0	0	7	9	16
45	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1
66	0	0	0	1	0	3	0	0	0	0	0	0	5	4	19
67	0	1	1	8	27	53	0	0	0	0	0	0	58	56	552
68	0	0	0	3	4	17	0	0	0	0	0	0	3	1	9
69	0	0	0	10	25	63	0	0	0	0	0	0	8	9	50
84	13	16	186	0	0	0	4	6	11	0	0	0	0	0	0
85	12	20	73	0	0	0	0	0	0	4	7	15	0	0	0
86	15	19	60	0	0	0	0	0	0	3	4	16	0	0	0
87	1	0	4	0	0	0	0	0	0	4	9	20	0	0	0
88	7	8	33	0	0	0	0	0	0	1	0	3	0	0	0
89	0	8	21	0	0	0	0	0	0	0	0	1	0	0	0
90	1	2	8	0	0	0	0	0	0	1	0	1	0	0	0
91	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0
92	3	4	13	0	0	0	0	0	0	1	0	1	0	0	0
104	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
105	55	75	246	0	0	0	3	1	4	1	0	1	0	0	0
106	29	45	138	0	0	0	0	0	0	3	5	14	0	0	0
107	52	81	200	0	0	0	8	12	42	3	5	9	0	0	0
108	34	43	126	0	0	0	1	6	13	9	12	30	0	0	0
109	134	160	497	0	0	0	1	3	5	29	19	93	0	0	0
110	44	69	151	0	0	0	1	2	5	22	12	58	0	0	0
111	70	112	292	0	0	0	1	3	7	5	5	23	0	0	0
112	91	122	507	0	0	0	0	0	0	31	53	231	0	0	0
113	229	268	1,681	0	0	0	0	0	0	75	81	507	0	0	0
114	111	128	375	0	0	0	0	0	0	149	147	587	0	0	0
115	15	6	52	0	0	0	0	0	0	7	10	36	0	0	0
124	9	19	32	0	0	0	0	0	0	0	0	0	0	0	0
125	64	87	310	0	0	0	105	112	416	0	0	0	0	0	0
126	20	29	89	0	0	0	24	29	109	0	0	0	0	0	0
127	42	55	214	0	0	0	100	118	597	0	0	0	0	0	0
128	25	30	103	0	0	0	39	40	120	0	0	0	0	0	0
129	42	45	294	0	0	0	30	26	90	0	0	0	0	0	0
130	10	7	36	0	0	0	1	0	3	2	1	6	0	0	0
131	63	93	239	0	0	0	18	14	40	29	34	85	0	0	0
132	72	99	305	0	0	0	0	0	0	25	31	97	0	0	0
133	6	4	18	0	0	0	0	0	0	19	20	239	0	0	0
134	6	4	24	0	0	0	0	0	0	20	22	97	0	0	0
167	2	1	6	0	0	0	0	0	0	0	0	0	0	0	0
108	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
169	1	0	4	0	0	0	0	0	0	0	0	0	0	0	0
150	7	11	29	0	0	0	17	12	35	4	11	21	0	0	0
151	0	0	2	0	0	0	0	0	0	1	0	1	0	0	0
Total	1,283	1,670	6,375	24	56	138	353	384	1,497	446	488	2,192	81	80	647

Table 2

Total kill of common, striped bottlenose, rough-toothed and unidentified dolphin species by sex (M = male, F = female) and geographic location (number of the corresponding 5° square shown in Figure 2). One short-finned pilot whale of unknown sex was taken in block 106.

	Common			Striped			Bottlenose			Rough-toothed			Unidentified		
5° block	M	F	Total	M	F	Total	M	F	Total	M	F	Total	M	F	Total
66	0	0	0	8	3	31	0	0	0	0	0	0	0	0	1
67	0	0	0	0	0	0	0	0	0	0	0	0	0	0	40
68	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
90	0	0	0	1	5	7	0	0	0	0	0	0	0	0	0
103	15	22	66	0	0	0	0	0	0	0	0	0	0	0	0
104	99	89	530	0	0	0	0	0	0	0	0	0	0	0	4
105	35	49	563	0	0	0	0	0	0	0	0	13	0	0	0
106	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
109	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
110	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
111	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
112	0	1	1	9	4	15	0	0	0	0	0	0	0	0	18
113	0	1	1	0	0	0	0	0	0	0	0	0	0	0	28
114	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9
124	3	5	19	0	0	0	0	0	0	0	0	0	0	0	0
125	0	0	0	0	0	0	0	1	2	0	0	0	0	0	14
126	0	0	0	0	0	0	2	3	6	0	0	0	0	0	0
127	0	0	0	0	0	0	6	2	15	0	0	0	0	0	22
128	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1
129	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10
130	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
131	0	0	0	1	2	3	0	0	0	0	0	0	0	0	10
134	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Total	152	167	1,180	19	14	5[illegible]	8	6	28	0	[illegible]	13	0	0	170

Table 3

Length frequencies of dolphins for which species/stock was known. Forty-four (44) spinner dolphins with stock unidentified were excluded. No kill was reported for coastal spotted dolphins.

	Northern offshore spotted		Southern offshore spotted		Eastern spinner		Northern whitebelly spinner		Southern whitebelly spinner		Common		Striped		Bottlenose	
Length (cm)	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
0-74	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
75-79	1	3	0	0	0	0	2	2	1	0	0	0	0	0	0	0
80-84	3	3	0	0	1	0	0	3	5	0	0	0	0	0	0	0
85-89	6	4	0	0	0	0	1	1	4	2	0	0	0	0	0	0
90-94	6	7	0	0	0	0	2	1	0	0	0	0	0	0	0	0
95-99	6	3	0	0	2	0	0	3	2	0	0	0	0	0	0	0
100-104	4	9	0	0	2	0	1	1	0	0	0	1	0	0	0	0
105-109	9	3	0	1	1	1	3	1	0	0	0	1	0	0	0	0
110-114	5	7	0	0	0	0	1	2	0	0	0	0	0	0	0	0
115-119	4	5	1	2	0	5	1	1	0	0	1	0	0	0	0	0
120-124	16	11	1	0	1	3	1	1	1	0	2	0	0	0	0	0
125-129	6	8	0	1	2	4	3	3	0	0	1	2	0	0	0	0
130-134	15	13	1	1	3	4	2	2	0	0	2	1	0	0	0	0
135-139	13	14	0	0	4	2	5	6	4	1	0	1	0	0	0	0
140-144	13	12	0	1	3	4	7	4	2	1	0	1	0	0	0	0
145-149	24	22	1	0	15	17	14	7	1	1	3	0	0	0	0	0
150-154	19	29	1	1	10	20	11	8	1	1	3	1	0	0	0	0
155-159	52	37	1	1	19	19	27	19	1	3	4	4	0	0	0	0
160-164	61	55	1	2	21	28	26	40	1	2	2	8	0	1	0	0
165-169	57	61	2	1	18	37	32	44	3	7	7	12	0	0	0	0
170-174	73	81	0	3	27	27	35	60	5	15	6	11	1	0	0	1
175-179	51	99	3	5	27	19	37	57	9	14	9	11	1	2	0	0
180-184	61	131	0	9	17	10	26	26	16	11	11	7	2	2	0	0
185-189	46	151	1	8	6	1	19	11	13	9	8	13	3	1	0	0
190-194	47	119	3	5	1	0	11	4	4	3	10	18	1	0	0	1
195-199	38	61	0	1	2	0	0	1	1	0	14	21	4	2	0	0
200-204	46	12	1	1	0	0	0	0	0	0	8	8	0	1	0	0
205-209	35	5	0	0	0	0	0	0	0	0	7	6	0	1	0	0
210-214	11	1	1	0	0	0	0	0	0	0	2	3	2	1	0	0
215-219	3	1	0	0	0	0	0	0	0	0	3	0	2	1	0	0
220-224	2	0	0	0	0	0	0	0	0	0	4	1	1	0	0	0
225-229	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0
230-234	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
235-239	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
240-244	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	716	968	18	43	182	201	267	309	74	70	109	131	18	12	0	2

Table 4

Reproductive condition of female dolphins for which reproductive samples were collected. 'Maturity undetermined' indicates that some life-history data (such as length) but not complete sets of gonads were collected.

	Northern offshore spotted		Southern offshore spotted		Eastern spinner		Northern whitebelly spinner		Southern whitebelly spinner		Common	
Reproductive condition	N	%	N	%	N	%	N	%	N	%	N	%
Maturity undetermined	256	25.9	12	24.5	62	30.5	66	21.4	17	22.4	20	15.2
Sexually immature	275	27.9	13	26.5	94	46.3	100	32.4	21	27.6	60	45.5
Sexually mature												
Pregnant only	134	13.6	3	6.1	13	6.4	25	8.1	6	7.9	9	6.8
Pregnant and lactating	19	1.9	2	4.1	2	1.0	5	1.6	1	1.3	14	10.6
Lactating only	201	20.4	11	22.4	25	12.3	74	23.9	18	23.7	25	18.9
Resting with a corpus luteum	17	1.7	0	0.0	0	0.0	2	0.6	2	2.6	2	1.5
Resting without a corpus luteum	74	7.5	5	16.3	5	2.5	32	10.1	9	11.8	2	1.5
Post-reproductive	6	0.6	0	0.0	0	0.0	1	0.3	1	1.3	0	0.0
Condition undetermined	5	0.5	0	0.0	2	1.0	4	1.3	1	1.3	0	0.0
Total	987	100.0	49	100.0	203	100.0	309	100.0	76	100.0	132	100.0

REFERENCES

Chivers, S.J., Hohn, A.A. and Miller, R.B. 1989. Composition of the 1987 incidental kill of small cetaceans in the US purse-seine fishery for tuna in the eastern tropical Pacific. *Rep. int. Whal. Commn* 39:315–9.

Chivers, S.J., Miller, R.B. and Hohn, A.A. 1990. Composition of the 1988 incidental kill of small cetaceans in the US purse-seine fishery for tuna in the eastern tropical Pacific. *Rep. int. Whal. Commn* 40:455–8.

Hall, M.A. and Boyer, S.D. 1986. Incidental mortality of dolphins in the eastern tropical Pacific tuna fishery: description of a new method and estimation of 1984 mortality. *Rep. int. Whal. Commn* 36:375–81.

Hall, M.A. and Boyer, S.D. 1987. Incidental mortality of dolphins in the eastern tropical Pacific tuna fishery in 1985. *Rep. int. Whal. Commn* 37:361–2.

Hall, M.A. and Boyer, S.D. 1988. Incidental mortality of dolphins in the eastern tropical Pacific tuna fishery in 1986. *Rep. int. Whal. Commn* 38:439–41.

Hall, M.A. and Boyer, S.D. 1989. Estimates of incidental mortality of dolphins in the eastern Pacific fishery for tropical tunas in 1987. *Rep. int. Whal. Commn* 39:321–2.

Hall, M.A. and Boyer, S.D. 1990. Incidental mortality of dolphins in the tuna purse-seine fishery in the eastern Pacific Ocean during 1988. *Rep. int. Whal. Commn* 40:461–2.

Henderson, J.R., Perrin, W.F. and Miller, R.B. 1980. Rate of gross annual production in dolphin populations (*Stenella* spp. and *Delphinus*) in the eastern tropical Pacific, 1973–1978. Southwest Fisheries Center, La Jolla, CA, Admin. Rep. LJ-80–02, 51pp.

Lo, N.C.H., Powers, J.E. and Wahlen, B.E. 1982. Estimating and monitoring incidental dolphin mortality in the eastern tropical Pacific tuna purse-seine fishery. *Fish. Bull., US* 80(2):396–401.

Oliver, C.W., Walker, G.J. and Miller, R.B. 1983. Time/area distribution and composition of the incidental kill of small cetaceans in the U.S. purse-seine fishery for tuna in the eastern tropical Pacific during 1981. *Rep. int. Whal. Commn* 33:603–15.

Perrin, W.F. and Oliver, C.W. 1982. Time/area distribution and composition of the incidental kill of dolphins and small whales in the U.S. purse-seine fishery for tuna in the eastern tropical Pacific, 1979–80. *Rep. int. Whal. Commn* 32:429–44.

Perrin, W.F., Coe, J.M. and Zweifel, J.R. 1976. Growth and reproduction of the spotted porpoise, *Stenella attenuata*, in the offshore eastern tropical Pacific. *Fish. Bull., US* 74(2):229–69.

Perrin, W.F., Scott, M.D., Walker, G.J. and Cass, V.L. 1985. Review of geographical stocks of tropical dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern Pacific. NOAA Technical Report NMFS 28 (unpublished). 28pp.

Wahlen, B.E., Walker, G.J., Miller, R.B. and Oliver, C.W. 1986. Composition of the incidental kill of small cetaceans in the US purse-seine fishery for tuna in the eastern tropical Pacific, 1982 through 1984. *Rep. int. Whal. Commn* 36:369–74.

Wahlen, B.E., Miller, R.B. and Macky, C.J. 1987. Composition of the incidental kill of small cetaceans in the US purse-seine fishery for tuna in the eastern tropical Pacific during 1985. *Rep. int. Whal. Commn* 37:353–5.

Wahlen, B.E., Miller, R.B. and Ladiana, S.J. 1988. Composition of the incidental kill of small cetaceans in the US purse-seine fishery for tuna in the eastern tropical Pacific during 1986. *Rep. int. Whal. Commn* 38:403–5.

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Antarctic Marine Living Resources (AMLR) program

The U.S. AMLR program: 1990–1991 field season activities

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The U.S. Antarctic Marine Living Resources (AMLR) program provides information needed to formulate U.S. policy on the conservation and international management of resources living in the oceans surrounding Antarctica. The program advises the U.S. delegation to the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR), part of the Antarctic Treaty system. One of the principal tenets of the CCAMLR treaty is that the harvest of living resources shall be managed with the goal of preserving species diversity and stability of the entire marine ecosystem. Because antarctic krill (*Euphausia superba*) are the dominant prey in the pelagic marine ecosystem, the effects of krill harvest on dependent predators must be thoroughly understood in order to manage the fishery within the mandate of CCAMLR.

The AMLR program monitors fin fish and krill fisheries, projects sustainable yields where possible, and formulates management advice and options. In addition, the program conducts field research designed to describe the functional relationships between antarctic krill, their predators, and key environmental variables.

The field research program is designed to investigate and refine two hypotheses:

- Krill predators respond to changes in the availability of their food.
- The distribution of krill is determined by physical, chemical, and biological characteristics of the pelagic habitat.

As in past seasons, the 1990–1991 AMLR field season included two components: first, a research cruise aboard the National Oceanic and Atmospheric Administration (NOAA) ship *Surveyor* in the waters surrounding Elephant Island, at the tip of the Antarctic Peninsula; and second, land-based studies at Seal Island, a small island next to Elephant Island, and at Palmer Station, a U.S. scientific station further south on the Antarctic Peninsula (figure 1).

The specific objectives of the field season were to

- map the physical structure of the upper 750 meters, including the thermohaline structure, oceanic fronts, water-mass boundaries, surface currents, eddies, and turbulent mixing;
- map the spatial distribution of phytoplankton biomass and phytoplankton production;
- map the spatial distribution of estimated krill biomass, including the horizontal and vertical variations in krill demography and growth; and
- describe reproductive success, feeding ecology, and growth rates of land-based krill predators throughout the reproductive season on Seal Island.

The *Surveyor* departed Punta Arenas, Chile, on 16 January 1991 to begin the first of two 1-month legs of the AMLR research cruise in the vicinity of Elephant Island. On 21 January a survey (survey A, figure 2) of the physical oceanography, biomass and productivity of phytoplankton, and distribution and condition of krill in the waters around Elephant Island, Clarence Island, and the eastern end of King George Island was initiated. The survey consisted of 1,100 miles of acoustic transects between 50 conductivity-temperature-density and net sampling stations. The survey was completed north of Elephant Island and finer scale acoustic mapping was conducted in an area of higher krill densities along the shelf/slope break. Two sites were selected for intensive MOCNESS (Multiple-Opening-Closing-Environmental-Sampling-System) sampling. A second survey (survey B) was then conducted, focusing on the area

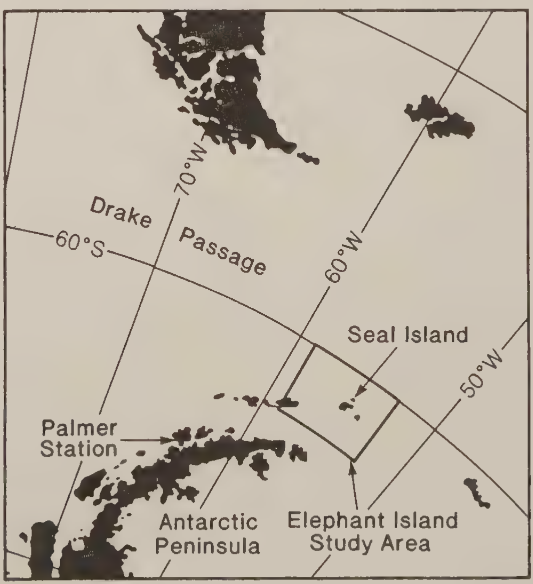

Figure 1. Antarctic Peninsula. Locations of Elephant Island study area, Seal Island, and Palmer Station shown.

north of Elephant Island. Two conductivity-temperature-depth transects were conducted to delineate the hydrography across the shelf/slope break. The *Surveyor* returned to Punta Arenas on 11 February 1991 for a mid-cruise port call.

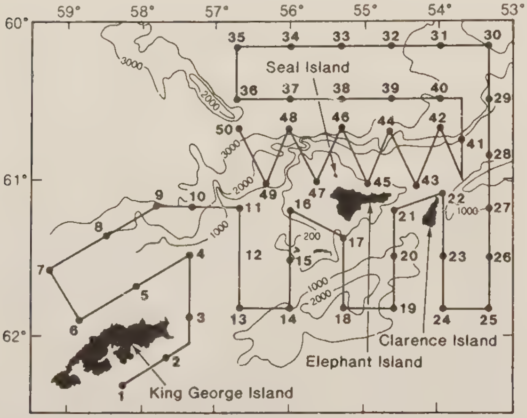

Figure 2. Large-area survey grid (surveys A and D) around Elephant Island, Clarence Island, and the eastern end of King George Island. The grid included 50 stations and approximately 100 nautical miles of transects and was occupied during the first half of leg I and the second half of leg II. Approximately 10 days were required to complete the grid.

Leg II of the AMLR cruise began on 16 February 1991. A third survey (survey C) was conducted north of Elephant Island; both bongo and IKMT (Issacs-Kidd Midwater Trawl) nets were used at each station. A final survey (survey D), which was similar in scale and scope to survey A (figure 2), was conducted from 26 February to 7 March 1991. Additional acoustic transects and stations were conducted in Bransfield Strait. The *Surveyor* returned to the north side of Elephant Island where MOCNESS sampling was directed at an area of high krill density along the shelf/slope break east of Seal Island. Two conductivity-temperature-depth transects were conducted across the shelf/slope break north of Elephant Island. The AMLR research cruise was completed on 17 March 1991 when the *Surveyor* returned to Punta Arenas, Chile.

A five-person field team arrived at Seal Island on 4 December 1990 to begin the land-based research of the 1990–1991 AMLR field program. In accordance with planned research objectives, the field team conducted extensive research on the reproductive and foraging behaviors of krill predators living on the island. Research on foraging behavior included tracking studies that were accomplished during cooperative research programs aboard the Japanese research vessel *Kaiyo Maru* in early January 1991, and aboard the Chilean research vessel *Alcazar* in mid-February 1991. The field team concluded their research activities on Seal Island on 11 March 1991.

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Current Analytic Concerns with Harvest Rate Management

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Abstract - Concerns with the implementation of harvest rate management can be lumped into two broad categories: strategic concerns - problems with the planning of a harvest rate management strategy, and tactical concerns - problems with actually carrying the strategy out. Strategic concerns are relevant for all management strategies while tactical concerns are more specific to harvest rate management. Strategic concerns include specification of a production function (stock-recruit relationship), estimation of stock productivity, and the problem of optimizing the harvest from fisheries that exploit both natural and hatchery fish. Harvest rate management was initiated for chinook salmon stocks of the Klamath River basin largely because of these strategic concerns. Implementation of harvest rate management has brought tactical concerns to the forefront. These include variability in the ocean distribution of Klamath basin stocks, unpredictability of the fishing industry response to attempts at managing harvest rates, and the imprecision of forecasts of the Klamath basin stocks. The future of harvest rate management will depend on the extent to which fisheries scientists are able to find solutions to these problems and the acceptability of the solutions to the management bodies and user groups.

When mathematicians speak of analytic problems they refer to problems that have analytic solutions. These are problems for which the solution can be expressed in closed form. The problems and concerns that I discuss here have no simple closed form solutions, but are concerns that relate to harvest rate management from the perspective of a fisheries analyst. These concerns can be divided into two broad categories: strategic concerns and tactical concerns. Strategic concerns are problems that relate to the development of a management strategy and tactical concerns are problems related to the implementation of the management strategy.

Strategic Concerns

All fisheries management depends on the premise that the per capita productivity of fish stocks is density dependent. When the density of a fish stock decreases, the growth rate of that stock increases, and when the density increases, the growth rate decreases. This means that if you harvest fish from a stock, the stock will tend to grow faster and will thus maintain itself, and if you stop harvesting a stock the growth rate will eventually slow so that the stock will not just continue to increase indefinitely. This density dependence is usually represented as a stock-recruitment relationship (SRR) which relates recruitment of fish in one generation to the spawning stock that produced it. We also know that any number of factors in addition to the size of the spawning stock influence recruitment and that this leads to variability about the SRR. However, in fisheries management, the size of the spawning stock is usually the only variable over which we have any direct control. If we can somehow characterize a stock's SRR, and the variability about it, then we can devise a harvest strategy that will optimize the yield from that stock.

There is no reason why the SRR of any stock of fish should be governed by any mathematical equation. Ideally what we would like to know is the probability distribution of recruitment for each possible spawning stock size. Unfortunately, if we picked just 10 stock levels and could somehow control the stock so that we could exactly achieve these levels, and we used just 10 recruitment observations to characterize the variability about the SRR at each stock level, it would take at least 100 years to accumulate the data, and by then the SRR would probably have changed. Instead, we assume some functional form for the SRR to reduce the amount of data required to estimate the relationship we are interested in.

The forms most commonly used in fisheries are the Ricker SRR

(1) $R = \alpha \times S \times \exp(-\beta \times S)$,

and the Beverton-Holt SRR

(2) $R = 1 / (\alpha - \beta \times S)$,

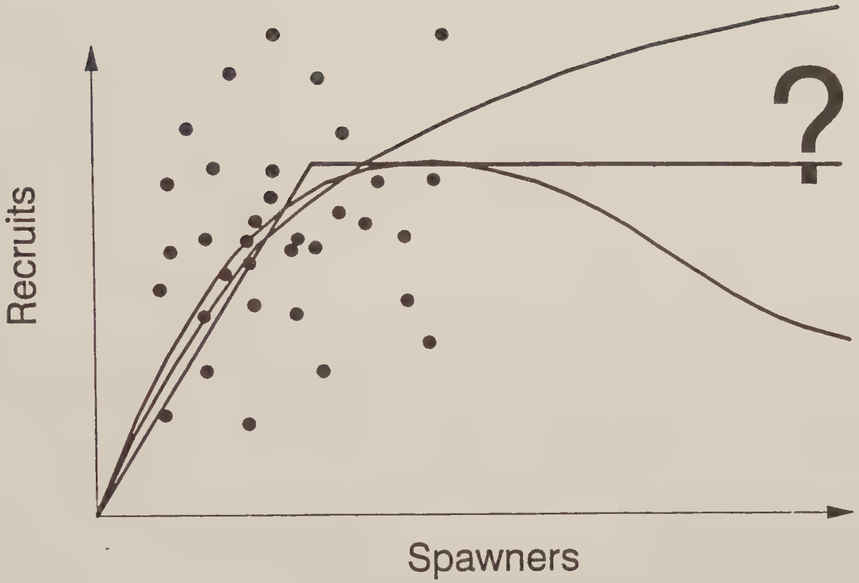

Figure 1. Variability in recruitment can lead to ambiguity in choosing between possible stock recruitment relationships. From top to bottom the curves are Beverton-Holt, rectilinear, and Ricker.

where R is recruitment, S is spawning stock, α is a parameter related to stock productivity, and β is a scaling parameter related to equilibrium stock size. These two forms can often similarly fit a stock and recruitment data set, but they can make very different predictions for stock levels outside the range of recent experience and have different implications for managing a fishery (Figure 1). In the event of a very abundant stock, the Beverton-Holt SRR predicts that under-harvesting the stock will produce a larger recruitment than harvesting the optimal yield. In the same situation, the Ricker recruitment curve predicts that under-harvesting may produce a much smaller recruitment. This difference can be substantial. It means that under-harvesting a stock governed by a Beverton-Holt SRR, you give up some harvest now, but you will be able to obtain a larger harvest in the future that will partially compensate for the loss. However, a Ricker SRR can carry a double penalty for under-harvesting in that you obtain a smaller harvest now and a smaller harvest in the future. Choosing between potential forms of SRRs can have substantial consequences on resulting management policy, but the choice is often hampered by the fact that most stock and recruitment data come from stocks that have been harvested down to where most mathematical forms for SRRs closely resemble each other.

Once an SRR is selected (usually a Ricker SRR for Pacific salmon), the key population characteristics from a management standpoint are estimated by fitting the SRR to a spawning stock and recruitment data set. Once fitted, the SRR can be used to estimate the optimal harvest rate and the spawning escapement that will, on average, produce the optimal harvest. There are a number of different methods for fitting the Ricker SRR, and for dealing with some of the biases in these techniques (Ricker 1975, Walters 1990), but the simplest method is the one most frequently used and it serves well to illustrate some of the problems with fitting SRRs. The Ricker SRR is usually fitted by taking the natural log of (1) and rearranging to obtain

(3) $\mathrm{Ln}(R/S) = \mathrm{Ln}(\alpha) - \beta \times S$.

The parameters α and β are then estimated by least-squares linear regression of Ln(R/S) on S. Because of the dynamics of the Ricker SRR and the fact that the data points used in the regression are not independent (the stock in one generation is the recruitment from the previous generation) the parameters estimated for a Ricker stock-recruit relationship are biased (Walters 1985, Kope 1988). The bias tends to overestimate the productivity of the stock and to underestimate the optimal spawning escapement, and increases as the variability in spawning stock levels decreases. The result is that when an SRR is fitted to a stock and recruitment data set from an over-harvested fishery, there is a built in tendency to perpetuate over-harvesting and depressed stock levels (Hilborn 1985a). The only way to gain more information about the shape of the SRR and to improve the estimates of parameter values is to increase the contrast in spawning escapements.

Fixed harvest rate management addresses these strategic concerns by allowing variation in spawning escapement that is proportional to the variation in recruitment. This variation can improve both the characterization of SRRs and estimation of parameters. Because the optimal harvest rate depends only on the productivity of the stock, and is independent of the equilibrium stock size (Hankin and Healey 1986), it may be possible to increase the accuracy of parameter estimates. In addition, depending on the management objective, fixed harvest rate management can be nearly optimal. If the management objective is to maximize the total expected harvest from a stock, then a constant escapement policy is optimal (Ricker 1958, Walters 1975). Such a management strategy is termed "risk neutral" because it ignores variability in harvests, and carries no penalty for the risk of having to shut down the fishery in the event that abundance falls below the optimal spawning escapement (Mendelssohn 1979). If a constant escapement strategy could actually be achieved, it would allow no variability in spawning escapement, and thus, provide no further information about the SRR except for the distribution of variability in recruitment at that spawning escapement level. When reasonable levels of productivity and variability in recruitment are considered, a constant escapement policy also results in no fishery about 5% to 10% of the time (Mendelssohn 1979). Recently, it has been argued that fishery management tends to be "risk averse" in that there is a tendency to stabilize harvests thereby reducing the risk of having to shut down the fishery (Mendelssohn 1979, Deriso 1985, Parma 1990). Risk averse management can be justified on the basis of sociological and economic impacts of fluctuations in harvest or obtaining no harvest, and is characterized by an increasing marginal value of

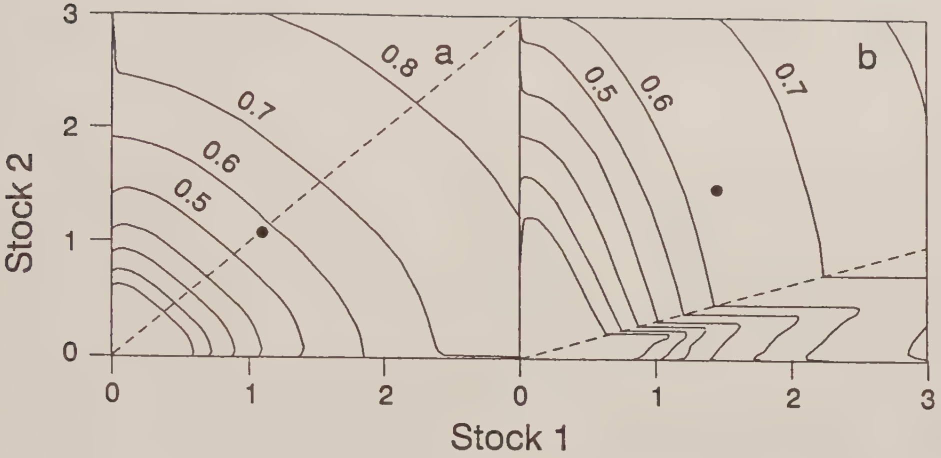

Figure 2. Optimal harvest rates for a 2-stock fishery with a risk neutral utility function for (a) 2 natural stocks governed by a Ricker SRR, and (b) a natural stock (stock 1) and a hatchery stock (stock 2) governed by a rectilinear SRR. The mixed-stock equilibrium producing MSY is indicated by a dot. The dashed line describes abundance combinations where the optimal mixed-stock harvest rate is also optimal for each stock individually.

harvest when harvest levels decrease (Deriso 1985). Constant harvest rate policies have been shown to be optimal, or nearly optimal, when the management objective is risk averse (Deriso 1985, Hilborn 1985b). In addition, by distributing variability between catch and escapement, constant harvest rate policies provide variability in spawning escapement necessary to improve estimates of stock productivity and adaptively manage for changing conditions (cf. Walters 1986).

Even if the SRRs are assumed to be known, estimating optimal harvest rates is complicated by the mixed stock nature of salmon fisheries. Optimal harvest rates can be calculated for each stock individually, but the fisheries, especially the ocean fisheries, harvest a mixture of stocks that differ in size, productivity, and origin. Using dynamic programming it is possible to calculate optimal harvest rates in a 2-stock fishery for different combinations of individual stock abundances, allowing for uncertainty about future stock dynamics (Hilborn 1976). These optimal harvest rates depend on the productivities and on the relative abundance of the two component stocks, but the degree of this dependence is strongly influenced by the form of the SRRs for the two stocks. If both stocks are governed by Ricker SRRs with similar productivities, as may be the case with 2 natural stocks from different rivers or different runs, optimal harvest rates are relatively insensitive to mixture of stocks that makes up a given abundance (Figure 2a). If we change the SRR of one of the stocks to simulate a hatchery stock by making it a rectilinear SRR with higher productivity, the optimal harvest policy depends very strongly on the relative abundances of the component stocks (Figure 2b).

Tactical Concerns

Once the decision was made to manage on the basis of fixed harvest rate, technical attention for the Klamath basin has focused on problems associated with implementing harvest rate management. As with strategic concerns, many of the problems associated with implementation stem from the multistock nature of the fisheries. Harvest rate goals have been set for Klamath Basin stocks, but the ocean fisheries harvest a mixture of stocks, of which the Klamath stocks are a component. In theory, by accounting for the ocean distribution of Klamath stocks, it should be possible to adjust harvest rates in different port areas to precisely obtain the desired harvest rate for Klamath stocks. However, in practice, regulating the fishing mortality rate is very difficult and imprecise.

There are basically two different approaches that can be taken to regulate the harvest rate in a fishery. The first is to try to manipulate the amount of fishing effort directed at the stock. This can be accomplished by limiting the number of participants in the fishery, implementing gear restrictions, fishing season closures, or any combination of these measures. The second approach is to limit harvest directly by setting landing quotas and shutting down fisheries when the quotas are reached. All of these tools are employed in the management of Pacific salmon fisheries. Within the Klamath Management Zone (KMZ), and in areas adjacent to the KMZ, commercial fisheries are regulated by a combination of seasonal closures and quotas in an attempt to limit impacts on Klamath stocks while providing access to other salmon stocks in the ocean. Some of the fisheries are of very short duration and restricted to small areas for the purpose of targeting specific stocks. Sport fisheries have operated under seasonal management with target quotas, and all fisheries are subject to gear and size restrictions.

The ocean distribution of Klamath chinook can be inferred from the pattern of recoveries of coded wire tags (CWT) from fish marked primarily at Trinity and Iron Gate hatcheries. Based on the recoveries of CWTs in past years it is possible to calculate the effects that changes in harvest rates in various portions of the coastal ocean will have on the overall harvest rate of Klamath chinook, assuming that the ocean distribution of salmon will be the same as in the base years. Operationally this accomplished using the Klamath Ocean Harvest Model (KOHM) discussed by Baracco and Dixon (this volume). The problems arise when we try to implement the harvest rate changes that we can evaluate relatively easily with the KOHM.

The first impediment to effectively regulating harvest rates is that the ocean distribution of Klamath Basin chinook changes year to year (Figure 3). It is readily apparent that in 1989 the Klamath stocks were distributed farther north than they were in 1986 and 1987. Because of the very low contribution rate of Klamath stocks to the fisheries south of the KMZ, in-season closures of the Fort Bragg fishery had very little effect on the overall harvest rate of Klamath stocks in 1989. Presently we have

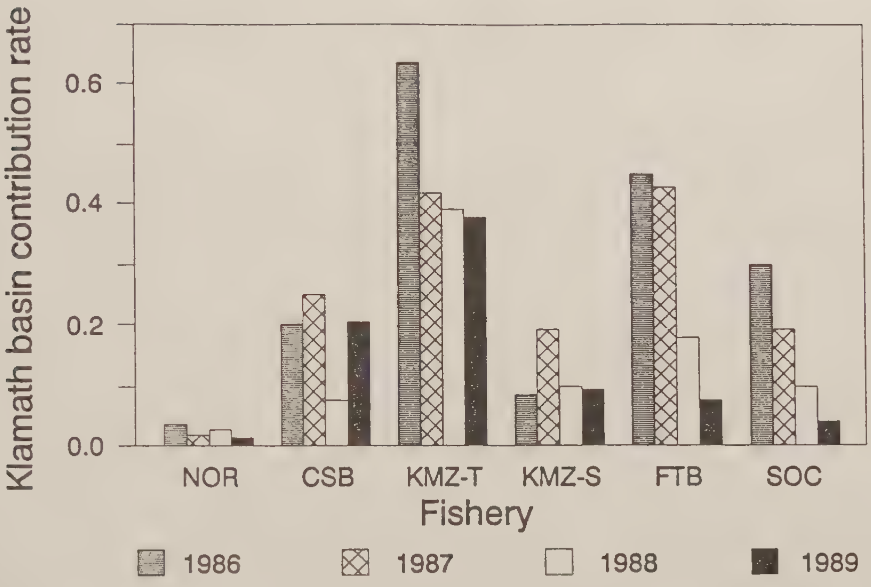

Figure 3. Fraction of chinook salmon landings originating from the Klamath basin as estimated by the recovery of coded-wire-tagged hatchery fish in northern Oregon (NOR), Coos Bay (CSB), Klamath management zone commercial fishery (KMZ-T), Klamath zone sport fishery (KMZ-S), Fort Bragg (FTB), and California ports south of Fort Bragg (SOC).

no way to anticipate the shifts in ocean distribution or to predict where the fish will be in any given year. Consequently, season structures and quotas that should, on average, produce the desired harvest rates on Klamath stocks may be ineffective in any specific year.

The second tactical problem is the difficulty of anticipating the fishing industry response to changes in regulations. When changes are made in the regulations to reduce the harvest rate, the response of fishermen is to adjust in some way so that the reduction in realized harvest rate is almost always less than anticipated. This difficulty may best be illustrate by a couple of examples. Within and adjacent to the KMZ some of the measures taken to try to decrease harvest rates have involved in-season closures. These in-season closures have typically been two weeks in duration and two weeks apart resulting in two weeks "on" and two weeks "off" for the industry. A proposal was made to change this to a weekly pattern of four days on and three days off, supported by the argument that this would still achieve the desired reduction in fishing effort while providing a more steady supply fish to help stabilize the market. This seemed to be a sound proposal, but examination of past closures revealed that in a two week period subject to the four day on

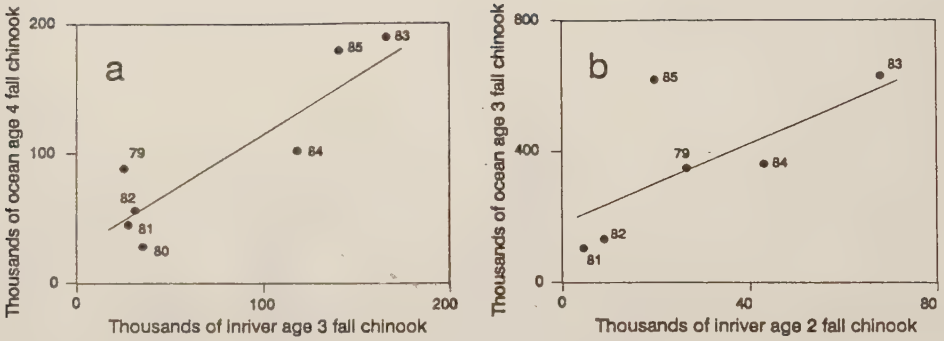

Figure 4. Regression relationships used to predict ocean abundance of Klamath basin stocks.

three day off schedule, boats fished an average of 76 hours out of a total of 112 hours available. During a comparable two week period when the season was open continuously, boats fished and average of 80 hours out of 210 available hours. A 47% reduction in the time available for fishing resulted in only a 5% decrease in the time spent fishing.

A second example is provided by the commercial fishery quotas in the KMZ. In 1988 the commercial troll fishery operated under a quota of 48,000 fish. The season opened on June 5 and was closed on June 7 after three days with the quota already exceeded because of a large influx of commercial boats into the KMZ to take advantage of abundant stocks there. In an effort to hold the ocean harvest rate down to levels dictated by the 1987 Klamath Fisheries Management Council (KFMC) harvest sharing agreement, the commercial chinook quota for 1989 in the KMZ was set at 22,500 with an in-season adjustment to 26,900 fish. Of this quota 17,700 fish were allocated to the June "all salmon" season. In an effort to make the season last longer, a trip limit of 20 fish was also implemented. In spite of the restrictive trip limit and chinook abundance that was lower than the preseason forecast, the season lasted only four days until the quota of 17,700 chinook was met.

Quotas have been employed in the KMZ because of the difficulty in regulating harvest rate by managing fishing effort. In theory, quotas directly limit the harvest rate by translating the desired target harvest rate into a quota and then shutting down the fishery when the quota is reached. The problem with quotas is that the desired harvest rate must be applied some forecast of abundance to generate the quota, and the accuracy of recent forecasts of Klamath chinook abundance has been perceived as less than satisfactory.

Abundance of each age-class of Klamath chinook is forecast separately from the run size of the corresponding age-class in the previous year. This method has worked relatively well for predicting age 4 abundance from 3-year-old spawners, but it has been less successful in

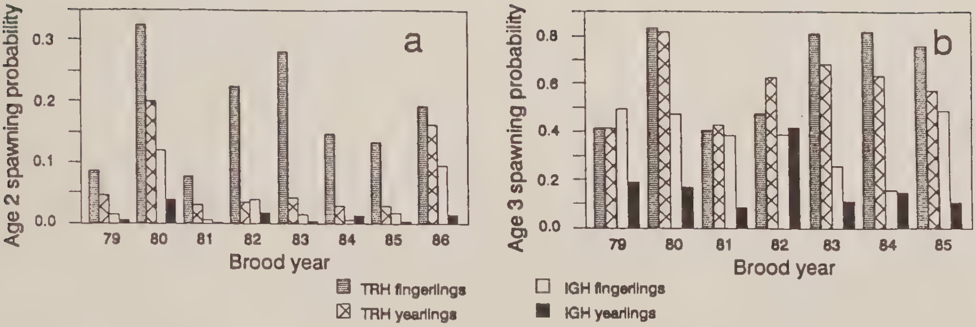

Figure 5. Maturation probabilities for 2-year-old and 3-year-old fish from Trinity River hatchery (TRH) and Iron Gate hatchery (IGH) for fingerling and yearling releases. Probabilities were estimated by cohort analysis of coded-wire tag recoveries.

predicting age 3 abundance (Figure 4). Unfortunately, 4-year-old fish are only a small portion of the Klamath stock in most years, with the bulk of ocean abundance composed of 3-year-old fish. This is due in part to the difficulty in enumerating 2-year-old spawners, and in part to the variability in the maturation rate of 2-year-old fish. Variability in maturation rate occurs among substocks and life history patterns as well as on a year to year basis (Figure 5, cf. Hankin 1990). This variability among substocks means that as the composition of the Klamath basin stock varies, the average maturation rate also changes, while the temporal variability further decreases the accuracy of forecasts. It is doubtful that our ability to forecast age 3 abundance will improve substantially in the near future. Improved forecasting will require including environmental variables in the forecasting process, and attempts to use environmental variables to improve stock forecasts have met with little success in the past. Even if forecasts can be improved, there is some question as to the utility of improved forecasting to fisheries management (Walters and Collie 1988).

Solutions

Optimizing a fixed harvest rate management policy requires only information on stock productivity while optimizing a fixed escapement policy require information about both productivity and equilibrium stock size. In theory then, harvest rate management should require less data than managing for fixed spawning escapement. Harvest rate management also adjusts automatically to changes in habitat capacity, and provides more information in the data collected from the fishery by increasing the contrast of observable levels of spawning escapement. For these reasons, harvest rate management seems preferable to fixed escapement management. Some of the problems with harvest rate management will certainly be addressed by the technical staffs of the management councils. As more data are collected from the fisheries we will learn more about the ocean distributions of various stocks both from CWT recoveries and from genetic stock identification. SRRs will continue to be refined as more data are collected from the spawning runs. If the recent diversity of management measures taken to try to regulate ocean harvest rates continues, we will gain a better understanding of the response to expect from the fisheries to future management. It may then be possible to manage on the basis of seasons rather than quotas, an option that most user groups would seem to prefer. However, both the commercial and sport troll fisheries have an excess of fishing power evidenced by the recent 3 and 4 day commercial seasons and a sport fishery in the KMZ that has exceeded the expected levels of effort and landings consistently in the last 4 years. Switching to seasonal management will probably entail substantial reductions in the fishing power of both the commercial and sport fishing industries if optimal harvest rates are to be obtained. While technical staffs may be able to provide recommendations and explore the implications of management options that may be considered in the future, the success or failure of harvest rate management will ultimately depend on the ability of the management councils to reconcile issues like harvest allocation, endangered species, and over-capitalization.

References

Deriso, R. B. 1985. Risk averse harvesting strategies. pp. 65-73 In Lecture Notes in Biomathematics No. 61. M. Mangel [ed.] Proceedings of the second Ralf Yorque workshop, Ashland Oregon. Springer-Verlag, New York.

Hankin, D. G. 1990. Effects of month of release of hatchery-reared chinook salmon on size at age, maturation schedule, and fishery contribution. Oregon Dept. Fish Wildl. Information Reports No. 90-4. 37 p.

Hankin, D. G., and M. C. Healey. 1986. Dependence of exploitation rates for maximum yield and stock collapse on age and sex structure of chinook salmon (*Oncorhynchus tshawytscha*) stocks. Can. J. Fish. Aquat. Sci. 43: 1746-1759.

Hilborn, R. 1976. Optimal exploitation of multiple stocks by a common fishery: a new methodology. J. Fish. Res. Board Can. 33:1-5.

Hilborn, R. 1985a. Apparent stock recruitment relationships in mixed stock fisheries. Can. J. Fish. Aquat. Sci. 42: 718-723.

Hilborn, R. 1985b. A comparison of harvest policies for mixed stock fisheries. pp. 75-87 In Lecture Notes in Biomathematics No. 61. M. Mangel [ed.] Proceedings of the second Ralf Yorque workshop, Ashland Oregon. Springer-Verlag, New York.

Kope, R. G. 1988. Effects of initial conditions on Monte Carlo estimates of bias in estimating functional relationships. Can J. Fish. Aquat. Sci. 45: 185-187.

Mendelssohn, R. 1980. Using Markov decision models and related techniques for purposes other than simple optimization: analyzing the consequences of policy alternatives on the management of salmon runs. Fish. Bull. 78: 35-50.

Parma, A. M. 1990. Optimal harvesting of fish populations with non-stationary stock-recruitment relationships. Natural Res. Modeling. 4: 39-76.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191. 382 p.

Walters, C. J. 1985. Bias in the estimation of functional relationships from time series data. Can. J. Fish. Aquat. Sci. 42 147-149.

Walters, C. J. 1986. Adaptive Management of Renewable Resources. Macmillan Publishing Company, New York. 374 p.

Walters, C. J. 1990. A partial correction factor for stock-recruitment parameter estimation in the presence of autocorrelated environmental effects. Can. J. Fish. Aquat. Sci. 47: 516-519.

Walters, C. J., and J. S. Collie. 1988. Is research on environmental factors useful to fisheries management? Can. J. Fish. Aquat. Sci. 45: 1848-1854.

Catch-per-effort and Stock Status in the U.S. North Pacific Albacore Fishery: Reappraisal of Both

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Abstract.–On reexamining a routine procedure for reporting catch-per-effort (CPE) in the North Pacific albacore fishery, we found evidence that CPE as an index of population size has been subject to a changing degree of bias. The increasing, positive bias in the routinely reported CPE has produced an optimistic, upward trend in this population index during the past decade. A time series of CPE, calculated in a different way, trends downwards. We show that both time series are subject to increasing, positive bias under conditions of an increasing ability of fishermen to locate concentrated patches of albacore. We present evidence that this ability has grown over the past decade, possibly as a result of increasing availability of satellite-based fishing advisories. The divergence of the two time series is explained by a model that shows a different rate of increase in bias in the two cases. The fact that the bias is increasing in the new time series implies that the true population has undergone a more severe decline than is shown by that series.

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The Southwest Fisheries Science Center (SWFSC) has been collecting fishery statistics from the U.S. North Pacific albacore fleet for a number of years. Overall catch-per-effort (CPE) and other summary statistics are included in the deliberations of the International North Pacific Albacore Workshops (Bartoo and Watanabe 1989) and are used to indicate the status of albacore stocks in the region. The history of these assessments has been consistently a favorable outlook of increasing abundance for the stocks, although in recent years the workshop has underscored the lack of detailed information about albacore catch in the growing gillnet fishery in the North Pacific.

The U.S. North Pacific albacore fleet consists primarily of jig vessels which vary in length from 25 to over 100 feet. The effect of vessel length on albacore fishing power was investigated by Laurs et al. (1976). They reported significant variability between 10-foot length-classes of jig vessels. Based on relative fishing power estimates for each year, adjusted effort and CPE values were calculated back to 1961. Since that time the calculation of fishing power and concomitant standardization of effort and CPE has become a routine part of reporting the albacore catch and effort statistics by the SWFSC.

In preparation for the 1989 North Pacific Albacore Workshop, we revisited the theory and rationale behind the effort standardization and calculation of CPE to see if the routine procedures continued to be appropriate. We found that even with standardization for fishing power, there was a high degree of residual variability in CPE within the fishing grounds which was not being addressed. Recalculation of the time series of CPE with a rough correction for such variability showed that the optimistic upward trend over the past decade in the original series was replaced by a downward trend. In an effort to reveal which of the two time series is more representative of the true course of the albacore population, we explored the data in more detail to find what might cause the divergence in the two CPE series. This paper is a report of our appraisal of the routine procedure and our reappraisal of the status of the albacore stocks.

Description of the fishery

The U.S. North Pacific albacore fishery is composed of several surface fishing gears. Trolling vessels (jig boats) are by far the most prevalent, followed by baitboats. They operate primarily in the eastern North Pacific. Other North Pacific fleets that harvest albacore include a Japanese baitboat fleet, operating in the western North Pacific, and wider-ranging Asian longline and gillnet fleets.

Except for the gillnet fleet, catch and effort in the surface fisheries has declined in the past 15 to 20 years. The U.S. commercial catch of albacore dropped from approximately 20,000 metric tons per year in the early 1970s to less than 5000 metric tons in the late 1980s, while effort dropped over the same period from 40,000 boat days to less than 5000 boat days.

The albacore are very patchily distributed, but evolving satellite technology has helped U.S. fishermen to locate areas of high concentration. Albacore tend to migrate along oceanic thermal fronts, and to form transient aggregations in areas where the frontal structures favor local enrichment (Laurs 1983, Laurs and Lynn 1977). These conditions are detectable by satellite (Laurs et al. 1984, Svejkovsky 1988). Over the past decade, increasingly sophisticated fishing advisories have been provided to fishermen. The advisories indicate, from satellite data, the locations of oceanographic conditions conducive to albacore aggregation, and fishermen have been taking increasing advantage of these advisories (Laurs 1989).

The ranges of the population and of the fishing grounds are variable both within the fishing season and from year to year. Albacore in the size range vulnerable to the U.S. fishery are entrained in an annual east-west migration pattern. The U.S. fishery peaks during the summer and autumn months when the albacore are closest to the North American coast. Albacore appear to be separated into northern and southern subgroups divided approximately by the 40°N latitude line (Laurs and Lynn 1977). The timing and extent of albacore migration are variable and without synchrony between the two subgroups. The location of oceanic fronts is also variable. As a result, the boundaries of the fishing grounds are extremely ill-defined and fluid, as is the extent to which the fishing ground overlaps the range of the albacore population. The traditional U.S. fishery is primarily nearshore. However, in the past 10 years, jig boats have been venturing farther offshore, some as far west as the dateline, earlier in the season in an attempt to meet the migrating albacore on their way toward the North American coast.

Theory and methods

The routine procedure for estimating fishing power in the U.S. albacore fleet makes use of a computer program, FPOW, coded by the California Department of Fish and Game and described by Fox (1971) and Berude and Abramson (1972). The basic theory behind this program is described by Robson (1966). The heart of the method is an analysis of variance which seeks to account for variation in the logarithm of CPE due to vessel length-classes, as well as to other factors such as time-area strata. Unlike usual analysis of variance, FPOW concentrates on reporting estimates of the coefficients in the statistical model. These coefficients are the logs of the fishing power of vessel classes relative to that of a reference class (45-foot vessels in this case). FPOW does not list a table of residual variances and F statistics, which would indicate the degree of statistical significance of the various factors. Accordingly, for the most recent year for which we had data (1988), we used a different analysis of variance program (BMDP) to better reveal the significance of variation due to vessel length in relation to other sources of variation.

As we looked into the routine procedure for aggregating catch and effort over all the time-area strata in a year, we found that effort (standardized for vessel length) and catch in the individual strata have been summed over strata, and a pooled CPE given by

$$\mathrm{CPE}_{\mathrm{pooled}} = \frac{\sum c_i}{\sum e_i} \qquad (1)$$

has been calculated, where c_i and e_i are the catch and effort in the i-th stratum. In the case where population density varies between strata, it is well known that such a pooled CPE is not a good population index because even though CPE might be proportional to population density in individual strata, that proportionality is destroyed with a pooled CPE. However, that proportionality can be maintained with a stratified CPE given by

$$\mathrm{CPE}_{\mathrm{strat}} = \frac{1}{N}\sum\left[\frac{c_i}{e_i}\right] \qquad (2)$$

where N is the number of strata (Beverton and Holt 1957:148–151). This is simply the average of CPE-s in individual strata. An effort aggregation scheme that in effect does the same thing has been used for the Japanese longline fishery for albacore (Honma 1974).

Strictly speaking, Equation 2 presumes that there is at least some effort in all strata. When that is not true, estimates should be provided of what CPE would have been in each of the missing strata had the fishery visited them. In the case of the U.S. North Pacific albacore fishery, the fluid nature of the fishing grounds described above makes it difficult to say whether a given stratum should be considered missing or not present in the fishing ground for a particular year. For the purpose of our new CPE series, we ignored the problem by ignoring unvisited strata. However, if the visited strata were not a random sample of available strata, the average CPE would be biased. To the extent that fishermen are able to locate strata with higher than normal population density, we expect them to favor those strata. Therefore, we expect that our new CPE values are only partially corrected for the effects of heterogeneous population density.

Either of the CPE series would still be useful, even though biased, as long as the bias does not change over time. But as noted above, the character of the fishery has been changing. The declining effort over the past approximately 20 years could lead to differential dropout of the less able fishermen, and the increasing availability and use of advisories in the past approximately 10 years could be increasing the ability of the remaining fishermen. The salient ability in this case is that of locating concentrations of albacore. If that ability has been changing, the bias in both old and new CPE time series must also be changing. We will show that the rate of change in bias is different in the two time series.

It would be useful to document the fact that the fishery is increasingly favoring high-abundance strata. Gulland (1956) suggested that the ratio of pooled to stratified CPE could be used as an index of effort concentration. But in this case we do not have a proper stratified CPE because of the problem of missing strata. We have devised a different favoritism index which is the proportion of the effort in any year that is expended in strata with a CPE above some threshold value, CPE*. The favoritism index in year y is given by

$$\text{favoritism index}_y = \frac{\sum_{i \in T_y} e_i}{\sum_{i=1}^{N_y} e_i};$$

$$T_y = \{i \mid (c_i/e_i) \geqslant \text{CPE}_y^*\} \qquad (3)$$

where T_y is the set of stratum indices for which CPE is greater than CPE_y^*, and CPE_y^* is determined by ranking the strata in year y according to CPE and choosing the minimum CPE of the top 20th percentile of the strata.

Data

Our data source is voluntarily contributed logbook information from the U.S albacore fishery. It is maintained on a database by the SWFSC and covers the years 1961 to 1989. The portion of landings sampled each year varies from 15% to 61%.

For analysis of variance, we used the 1988 data, the most recent year available at the time the analyses were conducted. As with the routine standardization procedure, we selected only jig boat records and organized the data by four large strata—early north, late north, early south, and late south—where the division between the early season and the late season is 1 September, and the division between north and south is 38°N latitude. Again following the routine procedure, within the large strata we treated the data by smaller time-area strata consisting of 3° latitude-longitude squares and half-month time periods, and classified vessels by 10-foot length classes. In contrast to the routine procedure, we maintained records of individual vessels within strata and length classes to allow analysis of variance with replicates. For calculating the CPE time series, we utilized 1° latitude-longitude strata, which is the finest resolution available.

Results and discussion

We conducted several analyses of variance with various subsets of the data, using CPE or ln(CPE) as the dependent variable.* Vessel length appears to be a significant factor in relatively few of these analyses (Table 1) whereas time-area stratum is almost always highly significant (low probability under H_0). Because the two-way analyses were unbalanced (unequal number of replicates), effects of the two factors could be confounded to some extent, and rigorous interpretation of the results is difficult. The salient features of the analyses are (1) that vessel size is of questionable significance as a factor influencing CPE, and (2) that time-area stratum tends to have a much higher statistical significance than does vessel size. In other words, it appears that vessel size does not matter nearly as much as where the vessel is and when.

Regardless of its statistical significance, the practical significance of vessel size in the context of reporting effort and CPE can be tested by seeing whether substantially different results are obtained with and without vessel size standardization. We recalculated the 1961 to 1989 time series without such standardization and found very little difference in CPE trends (Fig. 1). There appears to be little point in standardizing for fishing power even though vessel size may be statistically significant in some cases.

The emphasis on accounting for the effect of vessel size has obscured a more prominent feature of variability in CPE, which is the effect of location and time.

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* In the routine standardization, ln(CPE) is the dependent variable, and instances of zero catch with positive effort are ignored.

Table 1

Probability under H_0 (no effect) for vessel class (size) and time-area (strat) from one-way and two-way analyses of variance on various subsets of 1988 North Pacific albacore catch-and-effort data, and either CPE or ln(CPE + 1) as dependent variable.

	1- or 2-way	Source	Early season log(CPE+1)	Early season CPE	Late season log(CPE+1)	Late season CPE
North	1	size	0.15	0.001	0.46	0.42
	1	strat	<0.001	<0.001	<0.001	0.03
	2	size	0.03	<0.001	0.29	0.29
		strat	<0.001	<0.001	<0.001	0.03
South	1	size	0.009	0.035	0.66	0.48
	1	strat	<0.001	<0.001	0.22	0.84
	2	size	—	—	0.57	0.20
		strat	—	—	0.23	0.63

	1- or 2-way	Source	Whole season log(CPE+1)	Whole season CPE
North and South	1	size	<0.001	<0.001
	1	strat	<0.001	<0.001
	2	size	0.30	<0.001
		strat	<0.001	<0.001

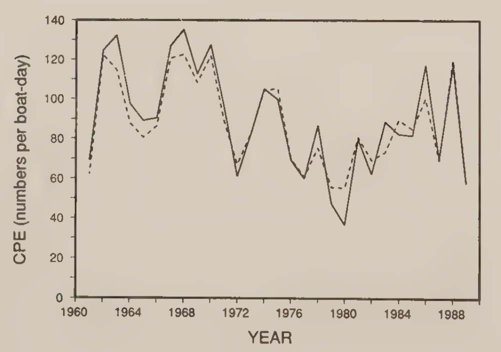

Figure 1

Comparison of original catch-per-effort time series (solid line) with unstandardized catch-per-effort (dashed line) for North Pacific albacore. Both time series are pooled catch-per-effort based on Equation 1. Effort values in the original time series are standardized for size of fishing vessels. Effort values in the other time series are not standardized.

This variability is not taken into account in the existing routine procedure. Our new time series, based on Equation 2 with unvisited strata ignored, gives a noticeably different picture (Fig. 2). The pronounced rising trend since 1978 in the old time series is replaced by a continuing downward trend.

The new CPE time series in Figure 2 was calculated without regard to the time sequence within a fishing season, that is, all spatio-temporal strata in a particular year were entered into the average for that year. If the fishery has not been fully covering the season in which albacore are available in the eastern Pacific, and if there has been a trend in the degree of coverage, then the yearly averages in Figure 2 could reflect that trend rather than a trend in the albacore population. We calculated a detailed time series with a separate CPE_{strat} for each 10-day period (Fig. 3) to look at the temporal pattern of CPE within seasons. In some years such as 1970, 1976, and 1989, it appears that the fishery may have missed a portion of the season of availability of albacore in the eastern Pacific. The CPE was already high at the beginning of the fishery, or the fishery quit before the CPE had tapered off. In most years, however, the fishery appears to have been active from the arrival of the albacore at the fishing ground to their departure. There does not seem to be a trend in the degree of coverage. In any case, it is not clear that variation in the degree of coverage would affect the old and new time series differently.

Another factor that might cause a divergence between the old and new time series of CPE would be an increasing ability of fishermen to locate areas of high albacore abundance. We will demonstrate that this is so with a simple model. Suppose there are two kinds of strata in the fishing ground, ones with low abundance and ones with high abundance, such that the population density within each type is d_l and d_h respectively, and $d_l<d_h$. We assume that CPE is proportional to fish density within the strata. Therefore we can measure d_l and d_h in catch-per-effort equivalents. Suppose further that there are n_l and n_h of each type of stratum in the fishing ground. If the fishery showed no favoritism for either type, then the probability of one unit of effort visiting any particular stratum would be $1/(n_l + n_h)$. We can model favoritism by defining p_l and p_h to be the probabilities that a unit of effort would visit a particular low-abundance or high-abundance stratum. We then let

$$p_l = \frac{1}{n_l + \alpha n_h}; \quad p_h = \frac{\alpha}{n_l + \alpha n_h} \qquad (4)$$

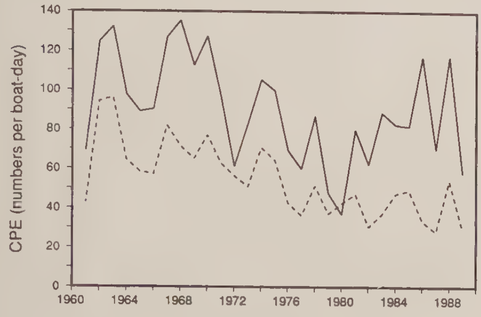

Figure 2

Comparison of original catch-per-effort time series (solid line) with a new catch-per-effort time series (dashed line) for North Pacific albacore. The original time series (CPE_{old}) is the same as the solid line in Figure 1. The new time series (CPE_{new}) is calculated using Equation 2 and ignoring strata with no effort.

where α is a favoritism coefficient. When α equals 1, the probability of a stratum of either type being visited is the same, and there is no favoritism. But as α increases, the chance for any high-abundance stratum is increased at the expense of the chance for any low-abundance stratum. Note that the sum of probabilities over all strata, $n_l p_l + n_h p_h$, is equal to 1, so that it is certain that a given unit of effort will land somewhere in the fishing grounds.

The probability that any particular stratum will receive a particular visit is $n_l p_l$ for low-density strata and $n_h p_h$ for high-density strata. The expected total number of visits is $e_{tot} n_l p_l$ to any of the low-density strata and $e_{tot} n_h p_h$ to any of the high-density strata, where e_{tot} is the total effort expended by the fishery. Therefore,

$$E[C_l] = e_{tot} n_l p_l d_l; \quad E[C_h] = e_{tot} n_h p_h d_h \qquad (5)$$

where C_l and C_h are the catches from all the low-density and high-density strata, respectively, and d_l and d_h are measured in CPE equivalents.

The old CPE is the total catch over total effort. Its expected value is thus,

$$E[CPE_{old}] = \frac{E[C_l] + E[C_h]}{e_{tot}} = n_l p_l d_l + n_h p_h d_h. \qquad (6)$$

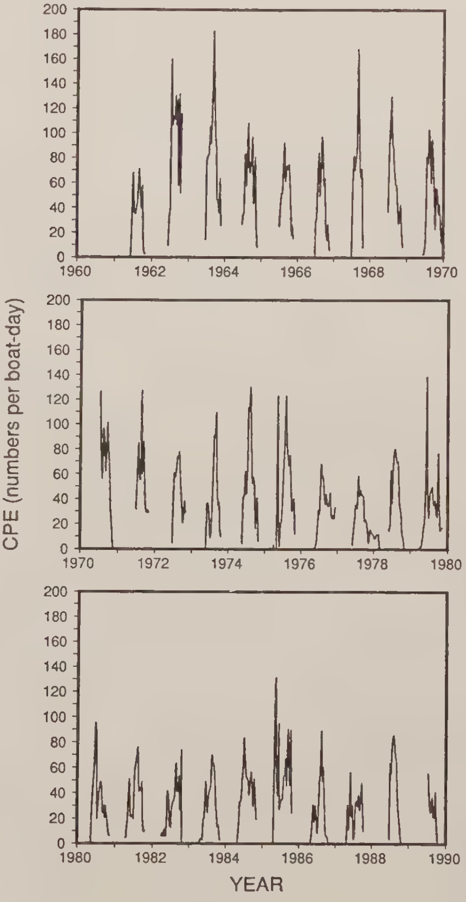

Figure 3

Detailed time series of stratified catch-per-effort for North Pacific albacore calculated for every ten-day period using Equation 2 and ignoring strata with no effort.

To calculate the new CPE, we need the number of strata in each area with at least one visit, v_l and v_h. To get these, we will first derive the number of low- and high-density strata that are missed altogether. The probability that a particular stratum is missed by a particular effort unit is $1 - p_l$ for low-density strata and $1 - p_h$ for high-density strata. The probability that a particular stratum is unvisited by any effort unit, that is, missing in the data, is thus,

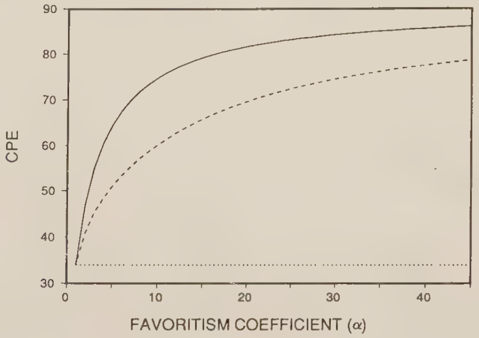

Figure 4
Catch-per-effort for North Pacific albacore predicted by model as function of favoritism coefficient, α, which reflects the ability of fishermen to locate fish concentrations. The expected values of CPE_{new} (solid line) and CPE_{old} (dashed line) are compared with the true mean population density in CPE equivalents (dotted line). The maximum error in the approximation for $E[CPE_{new}]$ is less than 0.7 CPE units in all cases.

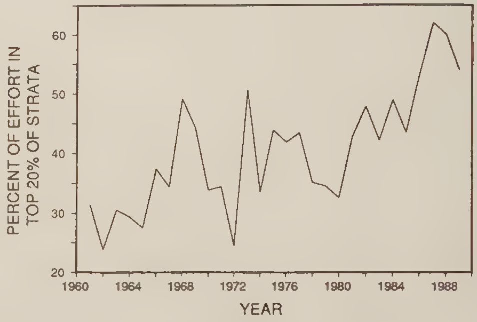

Figure 5
Favoritism index of vessels fishing for North Pacific albacore, calculated using Equation 3. The index measures the degree to which fishermen concentrate on strata with high fish populations. It is the proportion of effort in each year exerted in the top 20th percentile of strata where strata are ranked by catch-per-effort.

$$P[\text{stratum i missing}] = \begin{cases} (1-p_l)^{e_{tot}} & \text{if i in low-density area} \\ (1-p_h)^{e_{tot}} & \text{if i in high-density area.} \end{cases} \tag{7}$$

In each area the expected number of strata with at least one visit is the total minus the expected number of missing strata. Thus,

$$E[v_l] = n_l - n_l(1-p_l)^{e_{tot}}; \quad E[v_l] = n_h - n_h(1-p_h)^{e_{tot}}. \tag{8}$$

The new CPE is the average over the visited strata of the CPE values observed therein, that is,

$$CPE_{new} = \frac{v_l d_l + v_h d_h}{v_l + v_h}. \tag{9}$$

The functional form of Equation 9 does not allow substitution of expected values of v_l and v_h to get the expected value of CPE_{strat} exactly. However, it has been shown for a similar situation that it is a close approximation as long as the expected number of visited strata is not too small (Deriso and Parma 1988). The expected value of the new CPE is approximated by

$$E[CPE_{new}] \approx \frac{E[v_l]\, d_l + E[v_h]\, d_h}{E[v_l] + E[v_h]} \tag{10}$$

with an error less than $(d_l + d_h)/(E[v_l] + E[v_l])$ based on Deriso and Parma's formulation.

With some straightforward algebra it can be shown that when $\alpha = 1$ (no favoritism), $E[CPE_{old}]$ and $E[CPE_{new}]$ are both equal to the true mean population density (in CPE equivalents), that is,

$$\alpha = 1 \Rightarrow E[CPE_{old}] = E[CPE_{new}] = \frac{n_l d_l + n_h d_h}{n_l + n_h}. \tag{11}$$

It can furthermore be shown that as α increases above 1, $E[CPE_{old}]$ and $E[CPE_{new}]$ rise monotonically and approach d_h as α gets large (Fig. 4). Thus, old and new CPE are both unbiased when there is no favoritism; the bias increases at different rates for the two as favoritism increases; and they both approach the same bias as favoritism becomes large.

Relating the model results back to the U.S. North Pacific albacore fishery, we presume that an increasing ability to locate high-abundance strata is equivalent to a rising value of favoritism (α) in the model. The divergence of the old and new time series (Fig. 2) indicates that the effective α has been increasing toward some intermediate level. Changes in the fishery in the past decade—increasing availability and use of fishing advisories and severe decline in effort with the possibility of differential loss of less-able fishermen—are consistent with such a change in α.

In searching for corroborative evidence that the fishery has been increasingly concentrating on high-abundance strata, we found that the favoritism index given by Equation 3 has been tending upwards, particularly over the last decade (Fig. 5). This coincides well with the divergence in the old and new time series of CPE starting around 1979 (Fig. 2). Given this evidence of increasing ability to locate aggregations, the recovery in the old CPE time series in the past decade reflects a change in fishing operations and not a recovery of the albacore stocks. In fact, if the albacore population had just been holding its own over that time, the new time series should also have been rising because it is also subject to increasing positive bias. The fact that it has been declining indicates that the population must have been declining even more rapidly.

Though we have not invented a new population index, free of variable bias, the different effect of bias on our new CPE time series and the original CPE time series has helped reveal a change in fishing operations. This change has markedly affected our interpretation of CPE in the United States North Pacific albacore fishery. To reveal population trends with an unbiased time series requires that we deal with unvisited strata. The difficulties of doing so are great with the type of spatio-temporal variability that we have in the North Pacific albacore fisheries. Attempts are being made (R. Mendelssohn, NMFS Southwest Fish. Sci. Cent., Monterey, CA, pers. commun.) with the inclusion of fishery-independent data (environmental data in this case) to infer CPE in unvisited strata.

Conclusion

We have reexamined the details and justification for a routine procedure for processing catch-and-effort data from the U.S. Pacific albacore fleet. We have found that the use of estimates of fishing power to account for variation in catch rates due to vessel size is of negligible value. Standardizing effort for vessel size has had little effect on the observed time series of effort and CPE in this fishery.

On the other hand, the patchy distribution of albacore is of great importance. In the routine procedure for reporting overall fleet effort, the concentration of effort on areas of high abundance has been dealt with inappropriately, so that CPE trends are unrelated to trends in the population available to the fishery. The new CPE, which is an incomplete correction for concentration of effort, reverses what has been seen as a rising trend in abundance over the past decade.

We have shown that the divergence of the old and new time series is consistent with a fishery for a patchily distributed resource and a growing ability to locate high-density patches. Such a scenario is confirmed by detailed examination of changes in the distribution of catch and effort in the fishery. This change is probably due to increasing use of advisories aimed at locating dense albacore patches, but other possible contributing factors include the differential dropout of less-able fishermen from the fishery or a decreasing representation of less-able fishermen in the sampled landings. Whatever the cause, we have shown that in such a scenario, the original time series would have an increasing positive bias as an index of population, and the new series would also have an increasing positive, but reduced, bias. The nature of the fishery is such that we cannot calculate a reliably unbiased index of population based solely on the fishery data. However, the implication of our results is that the actual trend in the population should have been a more severe decline than is indicated by the new time series.

Citations

Bartoo, N., and Y. Watanabe
1989 Report of the eleventh North Pacific albacore workshop. Admin. Rep., LJ-89-24, Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA, 17 p.

Berude, C.L., and N.J. Abramson
1972 Relative fishing power, CDC 6600, FORTRAN IV. Trans. Am. Fish. Soc. 101:133.

Beverton, R.J.H., and S.J. Holt
1957 On the dynamics of exploited fish populations. U.K. Min. Agric. Fish., Fish. Invest. (Ser. 2) 19, 533 p.

Deriso, R.B., and A.M. Parma
1988 Dynamics of age and size for a stochastic population model. Can. J. Fish. Aquat. Sci. 45(6):1054.

Fox, W.W.
1971 User's guide to FPOW: A computer program for estimating relative fishing power and relative population density by the method of analysis of variance. Univ. Wash. Quant. Sci. Pap. 27, 6 p.

Gulland, J.A.
1956 A study of fish population by the analysis of commercial catches. Rapp. P.-V. Reun. Cons. Int. Explor. 130:21–27.

Honma, M.
1974 Estimation of overall effective fishing intensity of tuna longline fishery. Bull. Far Seas Fish. Res. Lab. (Shimizu) 10:63–66.

Laurs, R.M.
1983 The North Pacific albacore — An important visitor to California Current waters. Calif. Coop. Oceanic Fish. Invest. Rep. 24:99–106.
1989 Applications de la télédétection satellitaire du germon du Pacifique Nord, *Thunnus alalunga* (Bonnaterre). *In* Le Gall, J.-Y. (ed.), Télédétection satellitaire et pêcheries thonières océaniques. FAO Document technique sur les pêches 302. FAO, Rome, 148 p.

Laurs, R.M., and R.J. Lynn
1977 Seasonal migration of North Pacific albacore, *Thunnus alalunga*, into North American coastal waters: Distribution, relative abundance, and association with transition zone waters. Fish. Bull., U.S. 75:795.

Laurs, R.M., H.B. Clemens, and L.H. Hreha
1976 Nominal catch-per-effort of albacore, *Thunnus alalunga* (Bonnaterre), caught by U.S. jig vessels during 1961–70. Mar. Fish. Rev. 38(5):1–32.

Laurs, R.M., P.C. Fiedler, and D.R. Montgomery
1984 Albacore tuna catch distributions relative to environmental features observed from satellites. Deep-Sea Res. 31(9): 1085.

Robson, D.S.
1966 Estimation of the relative fishing power of individual ships. ICNAF Res. Bull. 3:5–14.

Svejkovsky, J.
1988 Remotely sensed ocean features and their relation to fish distributions. *In* Sproule, D.F., and G.S. Klepple (eds.), Marine organisms as indicators, p. 177–197. Springer-Verlag, NY.

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Growth, Mortality, and Movements of Juvenile California Halibut *Paralichthys californicus* in Shallow Coastal and Bay Habitats of San Diego County, California

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Abstract.–Growth and mortality rates were compared for juvenile California halibut *Paralichthys californicus* from bay and open coast habitats. Growth was estimated by determination of size-at-age using daily increments in otoliths. No significant difference was observed in size-at-age for juvenile halibut between 6 and 41 mm from the bays and open coast. However, age-specific mortality rates estimated for halibut <70 days were highest for newly-settled halibut on the open coast. California halibut settled either in bays or on the open coast, but ultimately nearly all of the halibut that settled on the coast entered and used the bays as nursery areas during their first year of life or else they died. The advantages of bays as nursery areas may be a decrease in risk of mortality of newly-settled halibut and an increase in growth of larger juveniles that feed upon the abundant small fishes in the bays.

The utilization of specialized nursery habitats by juvenile fish is a common phenomenon (Boehlert and Mundy 1988, Miller et al. 1986). Many of the fish species that utilize bays as nursery areas spawn in offshore waters, and move into bays as late larvae and early juveniles (Boehlert and Mundy 1988, Miller et al. 1986). The migration, location, and entry of larvae and juveniles into the bays involve complex behaviors that are particularly important on the Pacific coast of North America, where only 10–20% of the coastal habitat consists of estuaries and lagoons, compared with 80–90% on the Atlantic and Gulf coasts (Emery 1967). Possible consequences of the use of bays as nursery areas include faster growth because of high food production, warm temperatures, and decreased predation (Miller et al. 1986, Kneib 1987, Krygier and Pearcy 1986).

The California halibut *Paralichthys californicus* is a commercially important flatfish found in southern California coastal waters and bays (Frey 1971, Haaker 1975, Allen 1988, Love et al. 1986, Plummer et al. 1983). Eggs and larvae occur over the shelf and seaward, with greatest densities in waters less than 75 m deep and within 6 km of shore (Frey 1971, Gruber et al. 1982, Barnett et al. 1984, Lavenberg et al. 1986, Walker et al. 1987, Moser and Watson 1990). In past studies juvenile halibut rarely were taken on the open coast, suggesting that bays and lagoons might be the only significant nursery habitat (Plummer et al. 1983, Allen 1982, Kramer 1990).

The objective of this study was to determine the relative importance of bays as nursery areas and to evaluate the movements between bay and open coast habitats. To meet these objectives, I estimated habitat-specific distribution, abundance, and growth and mortality rates of juvenile halibut from both bay and open coast habitats.

Materials and methods

Distribution and abundance

California halibut were collected during a 2-year survey (September 1986–September 1988) of the open coast between Mission Bay and San Onofre, and two bays, Mission Bay and Agua Hedionda Lagoon (Fig. 1). A stratified random sampling design was used, consisting of four open coast blocks each with three depth strata (5–8 m, 9–11 m, and 12–14 m), and five blocks in Mission Bay and three blocks in Agua Hedionda Lagoon, each with three depth strata (0–1 m, 1–2 m, and 2–4 m) (Fig. 1).

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Fishery Bulletin, U.S. 89:195–207 (1991).

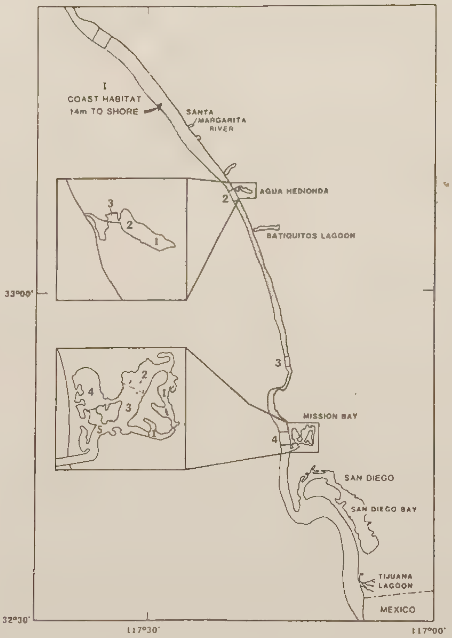

Figure 1

Location of sampling blocks. Open coast blocks are (1) San Onofre, (2) adjacent to Agua Hedionda Lagoon, (3) Torrey Pines, and (4) adjacent to Mission Bay. The two bays sampled are Agua Hedionda Lagoon and Mission Bay, with sampling blocks denoted.

For further description of the sampling design and the habitats see Kramer (1990).

Three gear types were used, all lined or made of 3-mm mesh: a 1.0-m wide beam trawl, a 1.6-m wide beam trawl, and a 1 × 6-m beach seine. The 1.6-m beam trawl, set from a 15-m research vessel, was used to sample the open coast and Mission Bay (Fig. 1). I sampled Agua Hedionda Lagoon and the areas of Mission Bay that were inaccessible to the larger vessel with the 1.0-m beam trawl, set from a 6-m skiff. The 1.0-m beam trawl and the beach seine were pulled along the bottom by two people to sample the shallow shoreline (<1 m) in the bays. The trawls were fitted with a wheel and revolution counter to determine the distance traveled by the trawl along the bottom, allowing a quantitative assessment of fish density since the trawls had a fixed mouth opening (Krygier and Horton 1975). All trawls and seines were fished during the day.

Table 1

Gear weighting coefficients and their variances by length-class for conversion of shoreline collections by beach seine and 1-m beam trawl. Coefficients determined by 3-way ANOVA between gear types, blocks, and months of sample on density for each length-class. Correction terms are given for length-classes with significant gear effects ($P \leqslant 0.05$). There were no significant gear effects in the 1.0–1.6 m beam trawls for open water tows.

Length class (SL, mm)	Correction term	Variance
26–30	3.291	0.124
31–35	4.398	0.319
36–40	2.752	0.099
41–45	4.699	0.359

All flatfishes taken in trawls and seines were measured to standard length (SL) in mm. Density of halibut in 5-mm standard length-classes was determined for juveniles ≤70 mm SL. The thirteen length-classes used were: SL≤10 mm, 11–15 mm, 16–20 mm, continuing to 66–70 mm SL. Abundance was determined by multiplying the mean density for each habitat by the area of each habitat.

Gear comparison

Densities based on the 1.0-m beam trawl collections did not differ significantly from those of the 1.6-m beam trawl for any length class (ANOVA, $P>0.05$, n 826). However, the beach seine captured significantly fewer small halibut (26–45 mm SL) than the 1.0-m beam trawl (Table 1). Since significant biases existed, density and abundance estimates of halibut were corrected for the differences in gear efficiency by weighting the mean density and variance for each length class where significant differences in catchability were found (Table 1).

The weighted mean density for each gear type was calculated as

$$d_w = (d_1 + gd_2)/(1 + g)$$

where d_1 = unweighted density, d_2 = weighted density, and g = weighting coefficient.

Estimated variance of the weighted mean d_w was calculated as

$$V(d_w) = V(d_1) + g^2V(d_2) + d_2^2V(g) + V(g)V(d_2)$$

where $V(d_1)$ = variance of unweighted density, $V(d_2)$ = variance of weighted density, and $V(g)$ = variance of weighting coefficient. Variance of the weighted mean was underestimated because the covariance terms were not included. Resampling techniques to estimate variance (e.g., bootstrap) were impractical because of the large size of the database.

Age validation and determination

Laboratory-reared halibut larvae of known age were measured to standard length in mm and their sagittae excised and mounted in resin (Eukitt, O. Kindler, West Germany) on a microscope slide. Age was estimated using the methods of Methot (1981) and Butler (1987). A microcomputer interfaced to an electronic digitizer was used to measure and count increments on a projected image of the otolith from a high-resolution video camera mounted on a compound microscope. Increment counts of 45 larvae (3.1–9.1 mm SL) that were reared at 16–20°C in the laboratory were regressed against the known age of the larvae to establish a relationship between estimated and known age. Increments were formed daily: the slope of the relationship (0.969) did not differ significantly from unity ($P>0.05$). The regression of the number of increments on age of halibut larvae (5–29 days) was

$$\text{Age (days)} = 3.496 + 0.969 \times (\text{no. increments})$$

where $r^2 = 0.981$, SE constant = 1.055, SE slope = 0.018, and range of increment counts = 1–26) (Fig. 2). Daily formation of rings has also been found in juveniles 30–70 mm SL (Kicklighter 1990). The first increment is deposited about 3.5 days after hatching, coinciding with the day of first feeding (Gadomski and Peterson 1988). I added 3.5 to the number of increments counted on the otolith so that age was equivalent to the number of days from hatching.

Ageing of field-caught halibut

Juvenile halibut from field collections were measured alive and either frozen or preserved in 80% ethanol. Sagittae were dissected and increments counted using the techniques described above. Sagittae from juveniles >20 mm SL were polished with 400- and 600-grit wet sandpaper before counting.

A total of 120 field-caught halibut were aged: 50 from Mission Bay, 19 from Agua Hedionda Lagoon, and 51 from the open coast. Larval sagittae are symmetrical and nearly circular (Fig. 3A), but after metamorphosis additional foci develop and the sagittae became asymmetrical, with maxiumum deposition along the rostral axis (Karakiri et al. 1989) (Fig. 3B). This shift in the axis of sagittal growth produces areas that are difficult to interpret (Fig. 3). These areas correspond to a period of about 7 days after metamorphosis. I estimated the number of increments in regions of transition between foci by counting the number of increments that occurred in an adjacent area on a different axis (Fig. 3). The relationship between standard length (mm) and otolith radius (μm) was linear for halibut >10 mm SL (Fig. 4).

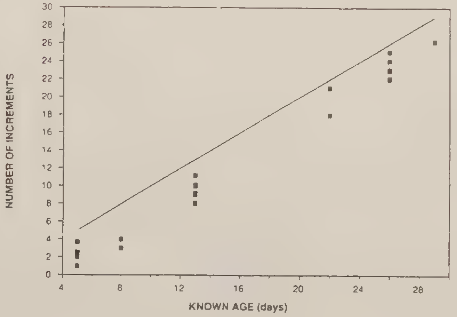

Figure 2
Age validation of California halibut sagittae. Number of increments counted on the sagittae are compared with the known age of laboratory-reared larval halibut (*n* 45). Straight line represents a one-to-one relationship of increment number and known age.

Mortality estimates

I did not use data from the 1987 survey for estimating mortality because nearly all of the 1987 year-class occurred in bays and comparisons of mortality between bay and coast habitats were an essential step in the analysis. The relationship between abundance and age (estimated from the length-at-age relationship) of the 1988 year-class was used to estimate age-specific mortality rates.

I used seven different models to estimate age-specific instantaneous mortality rates. Three of the models were estimates based on the following assumptions regarding the relationship between survival rates and age (Barlow 1982): (1) Age-specific survival rates increase linearly with age; (2) age-specific survival rates increase exponentially with age; and (3) age-specific survival rates approach an asymptote with age. The two daily production models estimated age-specific instantaneous mortality rates based on the relationship between daily production (abundance of length class/duration of length class) and age (Lo 1985). The last

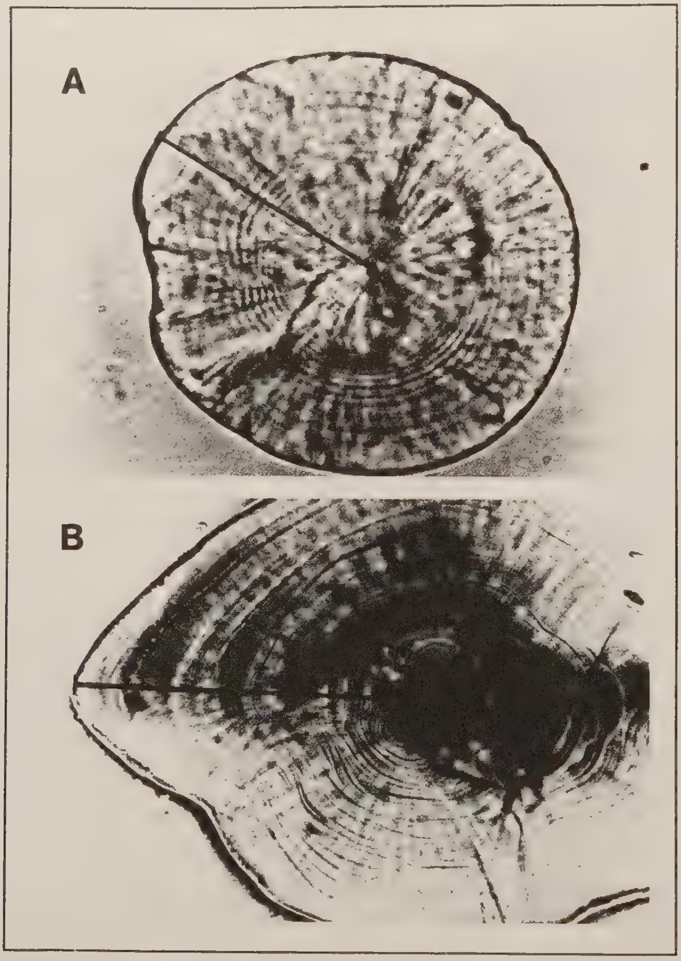

Figure 3
Photomicrographs of California halibut otoliths. (A) Sagitta from halibut 6.94 mm SL, estimated age 22 days. Distance of drawn radius, 70 µm. (B) Sagitta from halibut 48 mm SL, estimated age 109 days. Distance of drawn radius, 890 µm.

two models were simple linear estimates, using a linear regression of ln-transformed abundance-at-age on age (constant mortality rate with age) and on ln(age) (age-specific mortality rates). The sum of squared deviations of observed abundance-at-age from the calculated or transformed abundance-at-age predicted by each model was used to determine the model that best fit the data.

Mortality estimates for halibut from the open coast include loss of juveniles from the open coast population due to emigration into the bays. These estimates are used to calculate age-specific emigration rates by comparing the apparent mortality (= mortality + emigration) on the open coast to the total mortality calculated for the population on the open coast and in the bays.

Results

Effects of season and location on size-at-age

Relationships between halibut length and age did not vary significantly between seasons or between habitats. Analysis of covariance indicated no significant difference in length-at-age between fish that had birthdates in the spring and those with birthdates in the late summer and fall, but the sample size was small for fall fish (*n* 9) (Table 2). The common slope was 0.6206 (SE 0.0905).

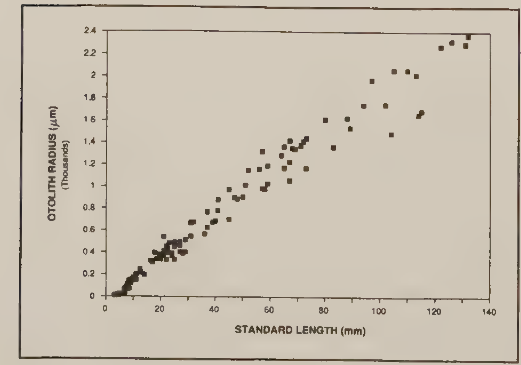

Figure 4
Relationship between otolith radius (µm) and standard length (mm) of California halibut (*n* 120).

Analysis of covariance also indicated no significant difference between juveniles from the bays and the open coast in the relationship between length and age (Table 2). The comparison was made between fish from the bays and the open coast. The common slope was 0.471 (SE 0.0238). Therefore, I used the pooled data for all estimates of growth (*n* 120).

Table 2

Regression analysis and analysis of covariance (ANCOVA) of size-at-age by season and by habitat. Slopes and intercepts were compared using ANCOVA; all tests were not significant at $P>0.05$.

Covariates	*N*	Size range (mm)	Equality of Intercept	Equality of Slope	*F*-statistic Intercept	*F*-statistic Slope
Seasons						
Spring	26	27–80	−7.6	0.637	1.68	0.051
Fall	9	27–83	−8.6	0.594		
Habitats						
Coast	51	6.8–41	−7.2	0.468	3.87	0.035
Bays	26	8.3–41	−4.7	0.478		

Length-at-age

The relationship between standard length (mm) and age (days) was best described with the Gompertz growth function,

$$\text{Length} = P_1 \times \exp(P_2(1-\exp(-P_3 \times \text{age})))$$

with $P_1 = 2.13$, $P_2 = 4.77$, and $P_3 = 0.011$, and an estimated mean square error of 0.99 ($2SE_{P_1} = 0.34$, $2SE_{P_2} = 0.137$, $2SE_{P_3} = 0.0013$) (Fig. 5A). The parameter P_1 closely estimates the length-at-hatching, which is 2.0 for halibut (Ahlstrom et al. 1984).

The relationship of age-at-length was determined with the function,

$$\text{Age} =$$

$$-88.347 \times \ln(\ln(\text{standard length} \times 251.07)/-4.769)$$

derived from the Gompertz relationship for size-at-age (Methot 1981) (Fig. 5B). The variance in the estimate of age-at-length increases with increasing length; the 95% confidence interval (CI) for a halibut age 25 days is ± 6 days, but for a 90-day-old halibut the 95% CI is ± 19 days (Fig. 5). This relationship was used to convert length-classes into age-classes using the mean of each length-class (Lo 1985).

I used the method outlined by Methot (1981, equations 1–5) to compute the age-specific daily growth rates. Length-specific daily rate of growth and the variability in growth rate increased with increasing length: the slowest growth occurred just after transformation (SL 6–10 mm), with daily growth <0.3 mm/day, and maximum growth rates of about 1 mm/day occurred in juveniles 70–120 mm SL (between 110 and 160 days) (Fig. 6). These growth rates are similar to those measured by Allen (1988) who estimated that juveniles 21–29 mm SL grew at 0.36 mm/day, and juveniles 19–47 mm SL grew at 0.99 mm/day.

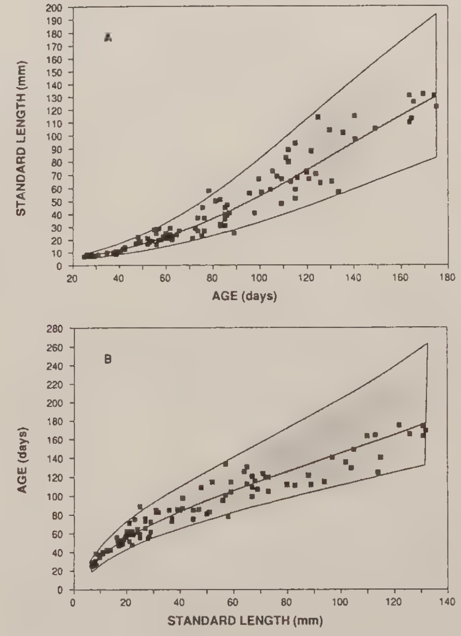

Figure 5

Gompertz relationship with 95% confidence intervals fitted to length-at-age of California halibut. (A) Standard length-at-age; (B) estimated age-at-length (mm).

Distribution and abundance

Juvenile California halibut 16–70 mm SL were present in the bays during January–July 1987 and March–September 1988, and on the open coast between May and September 1988. The distribution of transforming larvae and juveniles on the open coast differed for the 1987 and 1988 year-classes, with very few larvae and no small juveniles taken on the open coast in 1987

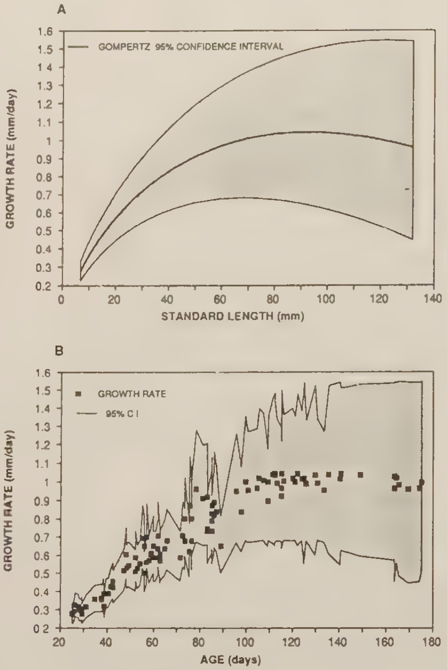

Figure 6
Growth rates of juvenile California halibut estimated from the Gompertz parameters for length-at-age, shown with 95% confidence intervals. (A) Relationship between growth rate (mm/day) and length (mm); (B) relationship between growth rate (mm/day) and age (days).

whereas transforming larvae and newly-settled juveniles were common in 1988. Only the 1988 year-class was used to compare growth and mortality rates for juvenile halibut in bays and on the open coast. Further information on the distribution patterns of juvenile California halibut can be found in Kramer (1990).

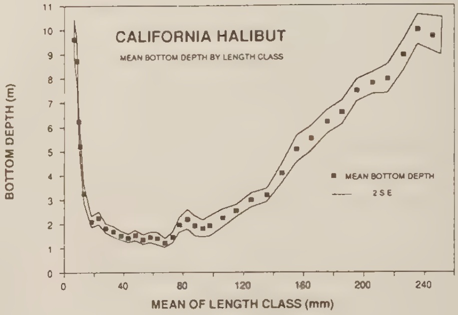

Figure 7
Mean depth of capture of California halibut by standard length-class (mm). Length-classes (mm) were ≤7 (*n* 54), 8 (52), 9 (47), 10 (38), 11–15 (116), 16–20 (198), 21–25 (161), 26–30 (161), 31–35 (116), 36–40 (116), 41–45 (138), 46–50 (127), 51–55 (124), 56–60 (92), 61–65 (81), 66–70 (92), 71–75 (74), 76–80 (45), 81–85 (53), 86–90 (50), 91–95 (42), 96–100 (53), 101–110 (74), 111–120 (103), 121–130 (101), 131–140 (154), 141–150 (154), 151–160 (109), 161–170 (129), 171–180 (143), 181–190 (121), 191–200 (135), 201–210 (128), 211–220 (88), 221–230 (73), 231–240 (60), and 241–250 (47).

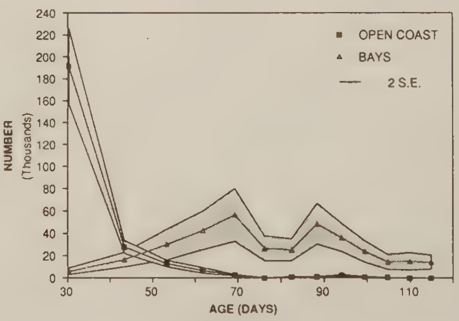

Figure 8
Abundance of juvenile California halibut by age-class for open coast and bay habitats in 1988.

The length distribution of transforming larval and juvenile halibut varied with depth. The smallest length-class of halibut (≤7mm SL) was taken at an average depth of 9.6m (SD 3.08, *N* 54). The mean depth of occurrence decreased with increasing length up to a mean length of 67.8mm SL (Fig. 7). At this size, the trend reversed, with mean depth of occurrence increasing with increasing length (Fig. 7). This pattern of length-at-depth indicates that transforming and newly-settled halibut move into shallower water along the open coast and into the bays, and halibut >70mm SL move into deeper water habitats within the bays (maximum bay depths were <5m) and eventually move out of the bays to the open coast (Fig. 7) (Plummer et al. 1983).

The age of peak abundance of juvenile halibut in the bays in 1988 was equivalent to the average time required for newly-hatched larvae to move from the continental shelf to the bays. Peak abundance was at about 70 days in both Mission Bay and Agua Hedionda

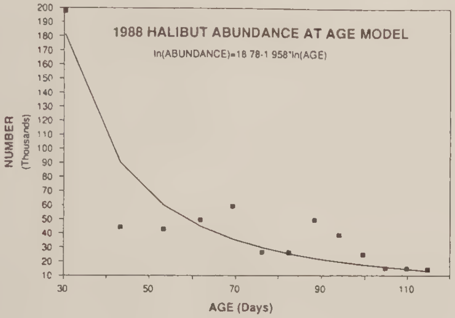

Figure 9

Total abundance of juvenile California halibut by age-class summed over both open coast and bay habitats, with the fitted model used to estimate mortality rates.

Table 3

Sum of squared deviations (SS) between observed and calculated or transformed abundance-at-age predicted from seven regression models applied to abundance-at-age for juvenile California halibut from 1988.

Model	Residual SS ($\times 10^9$)
1 Survival rate (SR) increases linearly $SR = 0.264 + 0.0072 * age$	6.48
2 Survival rate increases exponentially $SR = 0.174 * \exp((0.0070 * age) + 1.0035)$	7.99
3 Survival rate asymptotic $SR = 0.025 * age * \exp(-0.897)$	7.49
4 Daily production $\ln(\text{daily production}) = 17.1 - 1.54 * \ln(age)$	12.09
5 Daily production $\ln(\text{daily production}) = 9.55 - 0.0123 * age$	12.60
6 Log-transformed abundance on age $\ln(\text{abundance}) = 12.3 - 0.0229 * age$	10.87
7 Log-transformed abundance on ln(age) $\ln(\text{abundance}) = 18.78 - 1.958 * \ln(age)$	4.38

Lagoon ($N_{\text{Mission Bay}}$ 42,067, SE 8543; $N_{\text{Agua Hedionda Lagoon}}$ 14,432, SE 3312), but there was a second large peak in Mission Bay for individuals at about 90 days (*N* 43,697, SE 7850) (Fig. 8).

The class composed of transforming larvae (age 30 days) was the most abundant age class on the open coast in 1988 (*N* 191,553, SE 17,339) (Fig. 8). Abundance rapidly decreased with age on the open coast, with essentially no halibut 70–180 days of age present on the open coast (Fig. 8). The decline in abundance of halibut on the open coast corresponded to an increase in the bays (Fig. 8).

Mortality

Total age-specific abundance was determined by combining data from the bay and open coast habitats (Fig. 9). In the survey area, the total loss of juvenile halibut ages 30–115 days was estimated at 183,250 (95% CL of 148,800 and 210,350) (Fig. 9).

Instantaneous mortality rates ($z_{(t)}$) were calculated by age-class using abundance-at-age, with age obtained from the linear regression of ln-transformed abundance on ln(age) (Table 3, Fig. 9), and the duration of each age-class calculated from the age-at-size relationship (Table 4) (Lo 1985). Instantaneous mortality rates ($z_{(t)}$) were highest (0.044) for the youngest juveniles, and decreased with increasing age but became constant ($\bar{x}$ 0.0124, SD 0.001) for juveniles 70 days of age and older (Table 4).

I also calculated habitat-specific instantaneous mortality rates ($z_{(t)}$) for juveniles $\leqslant$70 days of age that were taken only on the open coast, and for those 88–115 days of age taken only in the bays (i.e., immigration completed (Table 5).

The apparent mortality in bays was much higher than that predicted from the combined bay and coast data, ranging from 0.043 to 0.037 for the bay model and from 0.011 to 0.014 for the total mortality model (Tables 4, 5). The age-specific mortality of halibut from the bays declined with increasing age, and was not constant as predicted by the total mortality model (Tables 4, 5).

To test for differences between the age-specific instantaneous mortality rates ($z_{(t)}$) of the total population, and of the open coast and bays, I used ANCOVA on the age-specific mortality coefficient, Beta. Beta is related to the instantaneous mortality rate ($z_{(t)}$) by the equation: $z_{(t)} = \text{Beta}/t$ (Lo 1985). The Beta coefficients for the total population (1.94, SE 0.22) and the open coast juveniles (ages $\leqslant$70 days, Beta 3.58, SE 1.10) were significantly different ($P \leqslant 0.01$) (Table 6). The difference in the Beta coefficient between juvenile halibut on the open coast and the total halibut abundance-at-age is probably due to movement of halibut from the coast to the bays. Nearly half of the decline in abundance of juveniles along the coast could be caused by their movement into the bays (1.94/3.58 = 0.54). The Beta coefficients for the total population and the bay juveniles (ages 94–115 days) also differed significantly ($P \leqslant 0.05$), with a Beta of 0.69 (SE 0.77) for the total population, and 2.96 (SE 0.65) for the juveniles from the bays (Table 6). Mortality rates in the bays appear to be underestimated by the abundance-at-age model for the total halibut population.

Table 4

Instantaneous mortality rates for the 1988 year-class of juvenile halibut <115 days ($z(t_i)$) by age in days (t_i) computed from daily juvenile production estimates (P_{ti}) and age (t_i) for 1988. Daily production estimates were obtained from log-linear model estimates of abundance-in-age classes adjusted for the number of days juveniles remained in the age-class. Percent of the total population in the bays by age-class is also given.

Length-class (SL, mm)	Age-class (t_i) (days)	Estimated abundance (*n*)	Percent in bays	Estimated daily production				
				P_{ti}	$P_{ti-1} - P_{ti}$	$t_i - t_{i-1}$	$t_i = (t_i + t_{i-1})/2$	$z(t_i)$
≤10	30.3	181385.1	3.08	18138.5				
11–15	43.3	90161.8	40.37	7706.1	10432.4	13.0	36.8	0.044
16–20	53.3	60025.3	69.92	6454.3	1251.8	10.0	48.3	0.016
21–25	61.8	44927.3	86.16	5615.9	838.4	8.5	57.5	0.015
26–30	69.3	35901.3	95.24	5056.5	559.4	7.5	65.5	0.013
31–35	76.2	29812.5	100.00	4586.5	469.9	6.9	72.7	0.013
36–40	82.5	25518.1	95.93	4183.3	403.2	6.3	79.3	0.013
41–45	88.4	22290.1	98.13	3910.5	272.7	5.9	85.4	0.011
46–50	94.1	19723.2	93.30	3586.0	324.5	5.7	91.2	0.014
51–55	99.5	17681.8	95.68	3336.2	249.8	5.4	96.8	0.012
56–60	104.8	15973.4	96.17	3132.0	204.2	5.3	102.1	0.011
61–65	109.9	14554.3	100.00	2910.8	221.2	5.1	107.3	0.013
66–70	114.9	13340.1	100.00	2722.4	188.4	5.0	112.4	0.012

Table 5

Habitat-specific instantaneous mortality rates of juvenile halibut <115 days ($z(t_i)$) by age in days (t_i) computed from daily juvenile production estimates (P_{ti}) and age (t_i) for 1988. Halibut 30.3–69.3 days of age were from the open coast habitat, and halibut ≥88.4 days were from the bays. Daily production estimates were obtained from log-linear model estimates of abundance by habitat adjusted for the number of days juveniles remained in each age-class.

Habitat	Age-class (t_i) (days)	Estimated abundance (*n*)	Estimated daily production				
			P_{ti}	$P_{ti-1} - P_{ti}$	$t_i - t_{i-1}$	$t_i = (t_i + t_{i-1})/2$	$z(t_i)$
Open coast	30.3	185384.8	18538.5				
	43.3	32540.9	2781.3	15757.2	13.0	36.8	0.065
	53.3	11820.4	1271.0	1510.3	10.0	48.3	0.054
	61.8	5746.9	718.4	552.6	8.5	57.5	0.051
	69.3	3288.5	463.2	255.2	7.5	65.5	0.048
	76.2						
	82.5						
Bays	88.4	45824.8	8039.4				
	94.1	33279.7	6050.9	1988.6	5.7	91.2	0.043
	99.5	25010.6	4718.9	1331.9	5.4	96.8	0.041
	104.8	19175.6	3759.9	959.1	5.3	102.1	0.038
	109.9	15035.1	3007.0	752.9	5.1	107.3	0.039
	114.9	11972.7	2443.4	563.6	5.0	112.4	0.037

Bay abundance-at-age estimate: $\ln(\text{abundance}) = 33.68 - 5.12 * \ln(\text{age})$ (residual SS = 4.567×10^7).
Open coast abundance-at-age estimate: $\ln(\text{abundance}) = 28.76 - 4.87 * \ln(\text{age})$ (residual SS = 6.219×10^7).

Table 6

Analysis of covariance (ANCOVA) on the age-specific mortality rate Beta by habitat, where Beta is defined by the relationship between the instantaneous mortality rate and age (z_t = Beta/t).

Covariates	*N*	Age range (days)	Beta	SE	*F*	*P*
Total population	4	43–69	1.94	0.22	19.62	<0.01
Coast population	4	43–69	3.58	1.10		
Total population	5	94–115	0.69	0.76	8.31	<0.05
Bay population	5	94–115	2.96	0.65		

Rate of movements into bays

I estimated the proportion of the population by age-class emigrating each day from the open coast to the bays by calculating the difference between the percentage of juvenile halibut lost daily from the total population and from the open coast using age-specific instantaneous mortality rates (Tables 4, 5) in the following equation:

$$\% \text{ emigrating/day } =$$

$$((1 - e^{-z(\text{total population})} - (1 - e^{-z(\text{open coast})})) \times 100.$$

The decline in abundance of juvenile halibut on the open coast between days 30 and 70 was 182,100, and for the total population was 145,500 (Tables 4, 5). During this time, the daily emigration rate increased from 1.99% for juveniles from age 30–43 days, to 3.67% from age 43–53 days, then declined slightly to 3.35% by 70 days.

Discussion

Extent of bay utilization

Juvenile halibut appear to be dependent upon bays as nursery areas, since nearly all halibut between 76 and 115 days of age occurred in the bays rather than the open coast (Fig. 8). Transforming larvae and newly-settled juvenile halibut ≤70 days old occurred on the open coast (97% of the transforming larvae were on the open coast), but over 95% of the total population of halibut >70 days were in the bays (Table 4).

An alternative explanation for the decline in abundance of juvenile halibut on the open coast is that they move somewhere other than the bays, or suffer heavy mortality. If halibut moved offshore, one would expect a positive relationship between size of juvenile halibut (31–70 mm SL, or 76–115 days) and bottom depth. This is contrary to the observed size-structured distribution pattern (Fig. 7). The decrease in abundance of juvenile halibut on the open coast may have included higher in situ mortality rates, but the corresponding increase in abundance in the bays suggests that movement from the coast to the bays probably accounts for about half of the coastal decline.

Advantage of bays as nursery areas

Growth The potential advantages of using bays as nursery areas are increased growth and decreased mortality. Increased growth was not observed for juvenile English sole *Parophrys vetulus* in Oregon estuaries: they grow at about the same rate as juveniles on the Oregon coast, but were more variable in size-at-age than those on the coast (Rosenberg 1982). Similarly, growth rates of juvenile California halibut ≤40 mm SL on the coast and in the bays were not significantly different.

California halibut 70–120 mm SL grew faster than all other length-classes with rates approaching 1 mm/day (Fig. 6). These fast and variable growth rates occurred during the period when juvenile halibut occurred only in the bays (>115 days of age). Unfortunately, comparisons could not be made between open coast and bay habitats during this period of fast growth, which coincides approximately with a change in the food habits of halibut >55 mm SL, from a diet composed primarily of small crustaceans (copepods, amphipods, mysids, and cumaceans) to one composed of an increasing proportion of fish by weight (mostly gobies) (Haaker 1975, Allen 1988, Drawbridge 1990). Juvenile halibut feeding on gobies in the laboratory remain partially buried in the substrate, only striking at gobies passing within a distance of three headlengths (Haaker 1975). Gobies are abundant in bays (mean density of *Ilypnus gilberti* in Mission Bay, 8.1/m^2), but not in shallow coastal waters <30 m (Brothers 1975, Allen 1985, Plummer et al. 1983). The diet of larger juvenile halibut becomes increasingly piscivorous: juvenile halibut >150 mm SL on the open coast eat primarily northern anchovies by weight (Plummer et al. 1983, Allen 1982).

Predation risk Predation risk may be higher for small halibut on the open coast than in the bays. At least six fish species on the open coast are known to eat flatfishes: these include California halibut, thornback ray *Platyrhinoidis triseriata*, fantail sole *Xystreurys liolepis*, bigmouth sole *Hippoglossina stomata*, speckled sanddab *Citharichthys stigmaeus*, and California lizardfish *Synodus lucioceps* (Ford 1965, Allen 1982). Ford (1965) found many small halibut (TL <10 mm) in the stomach contents of thornback rays, with a maximum of 15 newly-settled halibut in the stomach of one ray alone. The combined density of rays *Platyrhinoidis triseriata*, *Urolophus halleri*, and *Gymnura marmorata*) on the shallow open coast (<10 m) is about 100/hectare (Ford 1965). Speckled sanddab is the most abundant flatfish in shallow open coast waters, with a mean density of 950/hectare at Torrey Pines (Ford 1965, Allen 1982, Love et al. 1986, DeMartini and Allen 1984, Kramer 1990). Although the diet of speckled sanddab is composed primarily of mysids, they are probably capable of eating newly-settled halibut, since small unidentified flatfish juveniles have been found in their stomachs (Ford 1965).

In the bays, two potential predators include the round stingray *Urolophus halleri*, and the staghorn sculpin *Leptocottus armatus* (Allen 1985, Tasto 1975, Babel

1967). Both occur along the shallow open coast as well, but are most abundant in bays (Allen 1985). Staghorn sculpin feed primarily on crustaceans (>50% by weight), but small diamond turbot *Hypsopsetta guttulata* have also been found in their stomachs (frequency of occurrence 0.5%) (Tasto 1975). Over 94% of the diet by volume of round stingray is composed of molluscs, polychaetes, and crustaceans, but gobies also have been found in their stomachs (Babel 1967).

Other predators found both in the bays and on the open coast include barred sand bass *Paralabrax nebulifer*, spotted sand bass *P. maculatofasciatus*, and kelp bass *P. clathratus*. Spotted sand bass occur predominantly in bay habitats, barred sand bass occur ubiquitously in the bays and on the open coast, and kelp bass are associated with rock reef and kelp bed habitats on the open coast, but also have been taken as juveniles in bays (Allen 1985, Lane 1975). Kelp bass on the open coast feed mostly on northern anchovies and crabs, and have been found occasionally with flatfishes in their stomachs (Quast 1968). The diet of barred sand bass taken from bottom depths of 8–30 m on the open coast indicates that they forage close to the substrate, feeding on brachyuran crabs, mysids, pelecypods, and epibenthic fishes (mostly *Porichthys notatus*) (Roberts et al. 1984, Feder et al. 1974). Spotted sand bass occur predominantly in bay habitats, feeding on crabs and other crustaceans, and on small kelpfish (Feder et al. 1974, Allen 1985). The juveniles of all three species are found commonly in Mission Bay, and are considered highly probable goby predators (Brothers 1975). The sand basses probably eat juvenile halibut also, as gobies and halibut share the same habitats.

Comparison of predation risk must also include a measure of abundance or biomass of predators by habitat. The estimated density of the potential bay predators (round stingray, *Paralabrax* spp., and staghorn sculpin) based on otter trawl surveys is 61/hectare in Agua Hedionda Lagoon, and only 3/hectare on the open coast (San Diego Gas and Electric 1980). The estimated density of two open-coast predators, the speckled sanddab and the thornback ray, is >1000/hectare (Ford 1965). Based on this scanty information, it appears that predators are more abundant on the open coast than in the bays.

Thus the possible advantages of using bays as nursery areas by juvenile halibut appear to be at least twofold: (1) Decreased risk of predation on newly-settled juveniles, since fewer predators are known to occur there; and (2) increased potential for faster growth of juveniles >55 mm SL because small fishes (gobies) are more abundant in bays than on the open coast (Haaker 1975, Allen 1985).

Migration to bays

The migration of larvae from spawning areas over the continental shelf to their juvenile nursery areas in embayments is thought to consist of two phases (Boehlert and Mundy 1988): Accumulation of larvae in the nearshore zone (Boehlert and Mundy 1988, Miller et al. 1986), and location and entering of the bays by transforming larvae and juveniles (Boehlert and Mundy 1988). The nearshore accumulation of larvae prior to movement to the bays is probably facilitated by the timing of spawning, the short duration of pelagic stages, and the vertical distributions of the postflexion and transforming larval stages. California halibut spawn throughout the year, with peak spawning during the winter and spring (Lavenberg et al. 1986, Walker et al. 1987). The spawning peak coincides with the period of minimum offshore transport of surface water in the Southern California Bight (Parrish et al. 1981, Jackson 1986). Offshore transport increases in late spring and summer due to increasing upwelling activity (Parrish et al. 1981, Jackson 1986). The seasonal shift in upwelling activity has been correlated with a seasonal cross-shelf shift in the zooplankton assemblage off San Onofre: from February to early April the community was shifted onshore, and from mid-April to July the shift was offshore, corresponding to the period of increased upwelling (Barnett and Jahn 1987).

The size distribution of California halibut larvae taken in plankton tows indicates that they move inshore as they approach metamorphosis. Preflexion and flexion larvae (~2–6 mm SL) occur in midwater >2 km offshore, whereas transforming larvae occur at night in the neuston within 1 km of shore (Moser and Watson 1990). My collections indicated that transforming larvae occur on the bottom during the day; thus transforming larvae appear to undergo a daily vertical migration, occurring at the surface at night and at the bottom during the day. Larvae of other *Paralichthys* species, yellowtail flounder *Limanda ferruginea*, stone flounder *Kareius bicoloratus*, and the larval stages of several crustacean taxa have similar diurnal activity patterns (Weinstein et al 1980, Tsuruta 1978, Shanks 1988, Penn 1975, Smith et al. 1978).

Postflexion and transforming halibut larvae may be transported shoreward by internal waves at night when they are in the neuston, with very little movement during the day while they are on the bottom, resulting in accumulation of larvae nearshore (Moser and Watson 1990). Surface slicks associated with internal waves may transport neustonic larval fishes and crustaceans onshore (Shanks 1988, Kingsford and Choat 1986). Recovery of drift bottles released <20 miles offshore in the Southern California Bight region is greatest between March and October, also suggesting increased onshore transport of surface water (Schwartzlose 1963).

Once nearshore, transforming larvae or settled juveniles may search for bays by using longshore transport (Boehlert and Mundy 1988). Net longshore transport of shallow shelf waters in the Southern California Bight is to the south (Winant and Bratkovich 1981). Longshore current speed measured in shallow water (15 m) averages less than 5 cm/second; at this speed, after 12 hours longshore movement could be as great as 2 km (Winant and Bratovich 1981).

My data on the abundance of transforming larvae and newly-settled juveniles provide an estimate of the time required for halibut to locate and enter the bays from the open coast. The time required can be considered to be equivalent to the difference in the age of peak abundance between the coast and the bays. Halibut reached peak abundance in the bays at an age of about 70 days in 1988, whereas they were most abundant at age 30 days (transformation) on the open coast (Fig. 8). Thus the time required to locate and enter the bays was about 40 days in 1988 (70–30 = 40 days) (Fig. 8). Over a 40-day period, halibut potentially could be transported about 80 km alongshore (40 days × (2 km at 12 hours in the neuston)), which is greater than the total distance between the northern sampling block at San Onofre and Mission Bay (64 km) (Fig. 1). I measured the maximum distance between adjacent bays in southern California at less than 60 km, thus larvae using this transport mechanism would probably encounter a bay within 30 days of reaching the shallow-water coastal environment.

The potential cues used to find the entrances to bays include temperature, currents, odor, turbidity, and bottom substrate (Boehlert and Mundy 1988). A probable cue in southern California is temperature: during spring and summer, when larvae and juveniles are moving into the bays, the temperature is as much as 5°C warmer in the bays than on the open coast (Kramer 1990).

Once a bay entrance is located, the mechanism used to migrate into the bay probably is tidal transport, using incoming tidal currents to aid movement into the bay, and remaining at the bottom to avoid transport out of the bay (Weinstein et al. 1980, Boehlert and Mundy 1988, Fujii et. al. 1989, Tsuruta 1978, Weihs 1978, Runsdorp et al. 1985). To use tidal stream transport to move into bays, individuals must be able to orient to currents, control vertical movements, and remain on the bottom during unfavorable currents. These abilities probably develop by the time larvae reach transformation (Boehlert and Mundy 1988, Weinstein et al. 1980). Only a few tidal cycles may be required for halibut to move from the entrance into the bay. Larval flounder (*Paralichthys* sp.) on the North Carolina coast use tides to augment movement into marshes, migrating to the surface during night flood tides and remaining on the bottom during ebb tides and during the day (Weinstein et al. 1980).

In conclusion, California halibut settle either in bays or on the open coast, but ultimately nearly all halibut settling on the coast enter and use the bays as nursery areas during their first year of life. The advantages of bays as nursery areas may be a decrease in risk of mortality of newly-settled halibut, and an increase in growth of larger juveniles that feed upon the abundant small fishes in the bays.

Acknowledgments

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Citations

Ahlstrom, E.H., K. Amaoka, D.A. Hensley, H.G. Moser, and B.J. Sumida

1984 Pleuronectiformes: Development. *In* Moser, H.G., et al. (eds.), Ontogeny and systematics of fishes, p. 640–670. Spec. Publ. 1, Am. Soc. Ichthyol. Herpetol. Allen Press, Lawrence, KS.

Allen, L.G.

1985 A habitat analysis of the nearshore marine fishes from southern California. Bull. South. Calif. Acad. Sci. 84:133–155.

1988 Recruitment, distribution, and feeding habits of young-of-the-year California halibut (*Paralichthys californicus*) in the vicinity of Alamitos Bay–Long Beach Harbor, California, 1983–1985. Bull. South. Calif. Acad. Sci. 87:19–30.

Allen, M.J.

1982 Functional structure of soft-bottom fish communities of the southern California shelf. Ph.D. thesis, Univ. Calif. San Diego, 577 p.

Babel, J.S.

1967 Reproduction, life history, and ecology of the round stingray, *Urolophus halleri* Cooper. Calif. Dep. Fish Game, Fish. Bull. 137, 104 p.

Barlow, J.P.
1982 Methods and applications in estimating mortality and other vital rates. Ph.D. thesis, Univ. Calif. San Diego, 177 p.

Barnett, A.M., and A.E. Jahn
1987 Pattern and persistence of a nearshore planktonic ecosystem off southern California. Continental Shelf Res. 7:1–25.

Barnett, A.M., A.E. Jahn, P.D. Sertic, and W. Watson
1984 Distribution of ichthyoplankton off San Onofre, California, and methods for sampling very shallow coastal waters. Fish. Bull., U.S. 82:92–111.

Boehlert, G.W., and B.C. Mundy
1988 Roles of behavioral and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. Am. Fish. Soc. Symp. 3:51–67.

Brothers, E.D.
1975 The comparative ecology and behavior of three sympatric California gobies. Ph.D. thesis, Univ. Calif. San Diego, 370 p.

Butler, J.L.
1987 Comparison of the early life history parameters of Pacific sardine and northern anchovy and implications for species interactions. Ph.D. thesis, Univ. Calif. San Diego, 242 p.

DeMartini, E.E., and L.G. Allen
1984 Diel variation in catch parameters for fishes sampled by a 7.6-m otter trawl in southern California coastal waters. Calif. Coop. Oceanic Fish. Invest. Rep. 15:119–134.

Drawbridge, M.A.
1990 Feeding relationships, feeding activity and substrate preferences of juvenile California halibut, *Paralichthys californicus*, in coastal and bay habitats. M.S. thesis, San Diego State Univ., 214 p.

Emery, K.O.
1967 Estuaries and lagoons in relation to continental shelves. *In* Laugg, G.H. (ed.), Estuaries, p. 9–11. Am. Assoc. Adv. Sci. Publ. 83.

Feder, H.M., C.H. Turner, and C. Limbaugh
1974 Observations on fishes associated with kelp beds in southern California. Calif. Dep. Fish Game, Fish. Bull 160, 144 p.

Ford, R.E.
1965 Distribution, population dynamics and behavior of a bothid flatfish, *Citharichthys stigmaeus*. Ph.D. thesis, Univ. Calif. San Diego, 243 p.

Frey, H.
1971 California's living marine resources and their utilization. Calif. Dep. Fish and Game, Sacramento, 148 p.

Fujii, T., H. Sudo, M. Azeta, and M. Tanaka
1989 Settling process of larvae and juveniles of Japanese flounder, in Shijiiki Bay, Hirado Island. Nippon Suisan Gakkaishi 55:17–23 [in Jpn., Engl. abstr.].

Gadomski D.M., and J.H. Peterson
1988 Effects of food deprivation on the larvae of two flatfishes. Mar. Ecol. Prog. Ser. 44:103–111.

Gruber,D., E.H. Ahlstrom, and M.M. Mullin
1982 Distribution of ichthyoplankton in the Southern California Bight. Calif. Coop. Oceanic Fish. Invest. Rep. 23:172–179.

Haaker, P.L.
1975 The biology of the California halibut, *Paralichthys californicus* (Ayres) in Anaheim Bay. *In* Lane, E.D., and C.W. Hill (eds.), The marine resources of Anaheim Bay, p. 137–151. Calif. Dep. Fish Game, Fish. Bull. 165.

Jackson, G.A.
1986 Physical oceanography of the Southern California Bight. *In* Eppley, R.W. (ed.), Plankton dynamics of the Southern California Bight. Lecture notes on coastal and estuarine studies, p. 13–52. Springer-Verlag, NY.

Karakiri, M., R. Berghahn, and H. von Westernhagen
1989 Growth differences in 0-group plaice *Pleuronectes platessa* as revealed by otolith microstructure analysis. Mar. Ecol. Prog. Ser. 55:15–22.

Kicklighter, W.T.
1990 The relationship between somatic growth and temperature in the formation of otoliths by juvenile California halibut, *Paralichthys californicus*. M.S. thesis, San Diego State Univ., 76 p.

Kingsford, M.J., and J.H. Choat
1986 Influence of surface slicks on the distribution and onshore movements of small fish. Mar. Biol. (Berl.) 91:161--71.

Kneib, R.T.
1987 Predation risk and use of intertidal habitats by young fishes and shrimp. Ecology 68:379–386.

Kramer, S.H.
1990 Habitat specificity and ontogenetic movements of juvenile California halibut, *Paralichthys californicus*, and other flatfishes in shallow waters of southern California. Ph.D. thesis, Univ. Calif. San Diego, 266 p.

Krygier, E.E., and H.F. Horton
1975 Distribution, reproduction, and growth of *Crangon nigricauda* and *Crangon franciscorum* in Yaquina Bay, Oregon. Northwest Sci. 49:216–240.

Krygier, E.E., and W.G. Pearcy
1986 The role of estuarine and offshore nursery areas for young English sole, *Parophrys vetulus* Girard, of Oregon. Fish. Bull., U.S. 84:119–132.

Lane, E.D.
1975 Early collections of fishes from Anaheim Bay made between 1919 and 1928. *In* Lane, E.D., and C.W. Hill (eds.), The marine resources of Anaheim Bay, p. 13–15. Calif. Dep. Fish Game, Fish. Bull. 165.

Lavenberg, R.J., G.E. McGowan, A.E. Jahn, J.H. Peterson, and T.C. Sciarrota
1986 Abundance of southern California nearshore ichthyoplankton: 1979–1984. Calif. Coop. Oceanic Fish. Invest. Rep. 27:53–64.

Love M.S., J.S. Stephens Jr., P.A. Morris, M.M. Singer, M. Sandhu, and T.C. Sciarrotta
1986 Inshore soft substrata fishes in the Southern California Bight: An overview. Calif. Coop. Oceanic Fish. Invest. Rep. 27:84–106.

Lo, N.C.H.
1985 Egg production of the central stock of northern anchovy, *Engraulis mordax*, 1951–1982. Fish. Bull., U.S. 83:137–150.

Methot, R.D.
1981 Growth rates and age distributions of larval and juvenile northern anchovy, *Engraulis mordax*, with inferences on larval survival. Ph.D. thesis, Univ. Calif. San Diego, 203 p.

Miller J.M., L.B. Crowder, and M.L. Moser
1986 Migration and utilization of estuarine nurseries by juvenile fishes: An evolutionary perspective. *In* Rankin, M.A. (ed.), Migration: Mechanisms and adaptive significance. Contrib. Mar. Sci. Univ. Tex. suppl. vol. 27:338–352.

Moser, H.G., and W. Watson
1990 Distribution and abundance of early life history stages of the California halibut, *Paralichthys californicus* and comparisons with the fantail sole, *Xystreurys liolepis*. Calif. Dep. Fish Game, Fish. Bull. 174 (in press).

Parrish, R.H., C.S. Nelson, and A. Bakun
1981 Transport mechanisms and reproductive success of fishes in the California Current. Biol. Oceanogr. 1:175–203.

Penn, J.W.
1975 The influence of tidal cycles on the distributional pathway of *Penaeus latisulcatus* Kishinouye in Shark Bay, Western Australia. Aust. J. Mar. Freshwater Res. 26:93–102.

Plummer, K.M., E.E. DeMartini, and D.A. Roberts
1983 The feeding habits and distribution of juvenile-small adult California halibut (*Paralichthys californicus*) in coastal waters off northern San Diego County. Calif. Coop. Oceanic Fish. Invest. Rep. 24:194–201.

Quast, J.C.
1968 Observations on the food and biology of the kelp bass, *Paralabrax clathratus* with notes on its sportfishery at San Diego, California. *In* North, W.J., and C.L. Hubbs (eds.), Utilization of kelp-bed resources in southern California, p. 81–108. Calif. Dep. Fish Game, Fish. Bull. 139.

Roberts, D.A., E.E. DeMartini, and K.M. Plummer
1984 The feeding habits of juvenile-small adult barred sand bass (*Paralabrax nebulifer*) in nearshore waters off northern San Diego county. Calif. Coop. Oceanic Fish. Invest. Rep. 25: 105–111.

Rosenberg, A.A.
1982 Growth of juvenile English sole, *Parophrys vetulus*, in estuarine and open coastal nursery grounds. Fish. Bull., U.S. 80:245–252.

Runsdorp, A.D., M. van Stralen, and H.W. van der Veer
1985 Selective tidal transport of North Sea plaice larvae *Pleuronectes platessa* in coastal nursery areas. Trans. Am. Fish. Soc. 114:461–470.

San Diego Gas and Electric
1980 Encina power plant cooling water intake system demonstration. San Diego Gas and Electric, San Diego, CA.

Schwartzlose, R.A.
1963 Nearshore currents of the western United States and Baja California as measured by drift bottles. Calif. Coop. Oceanic Fish. Invest. Rep. 9:15–22.

Shanks, A.L.
1988 Further support for the hypothesis that internal waves can cause shoreward transport of larval invertebrates and fish. Fish. Bull., U.S. 86:703–714.

Smith, W.G., J.D. Sibunka, and A. Wells
1978 Diel movements of larval yellowtail founder, *Limanda ferruginea*, determined from discrete depth sampling. Fish. Bull., U.S. 76:167–178.

Tasto, R.N.
1975 Aspects of the biology of Pacific staghorn sculpin, *Leptocottus armatus* Girard, in Anaheim Bay. *In* Lane, E.D., and C.W. Hill (eds.), The marine resources of Anaheim Bay, p. 123–135. Calif. Dep. Fish Game, Fish. Bull. 165.

Tsuruta, Y.
1978 Field observations on the immigration of larval stone flounder into the nursery ground. Tohoku J. Agric. Res. 29:136–145.

Walker, H.J. Jr., W. Watson, and A.M. Barnett
1987 Seasonal occurrence of larval fishes in the nearshore Southern California Bight off San Onofre, California. Estuarine Coastal Shelf Sci. 25:91–109.

Weihs, D.
1978 Tidal stream transport as an efficient method for migration. J. Cons. Cons. Int. Explor. Mer 38:92–99.

Weinstein, M.P., S.L. Weiss, R.G. Hodson, and L.R. Gerry
1980 Retention of three taxa of postlarval fishes in an intensively flushed tidal estuary, Cape Fear River, North Carolina. Fish. Bull., U.S. 78:419–436.

Winant, C.D., and A.W. Bratkovich
1981 Temperature and currents on the southern California shelf: A description of the variability. J. Phys. Oceanogr. 11:73–86.

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THE SHALLOW-WATER FLATFISHES OF SAN DIEGO COUNTY

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ABSTRACT

Seven species of flatfish live in the shallow marine waters (depth 14 m) of San Diego County: California halibut, *Paralichthys californicus*; fantail sole, *Xystreurys liolepis*; speckled sanddab, *Citharichthys stigmaeus*; spotted turbot, *Pleuronichthys ritteri*; hornyhead turbot, *Pleuronichthys verticalis*; diamond turbot, *Hypsopsetta guttulata*; and California tonguefish, *Symphurus atricauda*. Speckled sanddab was most abundant, representing 79% of the flatfish catch. California halibut had the highest biomass, and represented 46% of the catch.

Only California halibut and diamond turbot used bays as nursery areas; they had distinct ontogenetic distributions, with length increasing with depth. The remaining species settled on the open coast but were not found together during early juvenile stages; they settled at different depths, and at different times of the year. Older juveniles and adults partitioned the habitat by eating different foods and by living at different depths and locations.

Life histories of nearshore flatfishes varied widely: speckled sanddab settled at a large size on the open coast and matured rapidly, whereas California halibut settled at a small size, used bays as nurseries, and delayed maturity.

RESUMEN

Siete especies de lenguados viven en aguas marinas someras (profundidad de 14 m) en el condado de San Diego: *Paralichthys californicus, Xystreurys liolepis, Citharichthys stigmaeus, Pleuronichthys ritteri, P. verticalis, Hypsopsetta guttulata,* y *Symphurus atricauda*. *Citharichthys stigmaeus* fué la especie mas abundante representando un 79% de la captura de lenguado. *Paralichthys californicus* presentó la mayor biomasa y un 46% del lenguado capturado.

Solamente *Paralichthys californicus* y *Hypsopsetta guttulata* utilizaron bahías como zonas de cría. Estas dos especies presentan distribuciones características durante la ontogénesis, con aumento de longitud del individuo con profundidad. Las otras especies se establecieron en la costa pero no coincidieron durante los períodos juveniles más tempranos: se establecieron a diferentes profundidades, y en tiempos del año diferentes. Los juveniles más viejos y los adultos dividieron el habitat comiendo alimento diferente y viviendo a profundidades y localidades diferentes.

Los ciclos de vida de los lenguados en aguas de poca profundidad variaron ampliamente: *Citharichthys stigmaeus* se estableció después de alcanzar tamaño grande y maduró rapidamente, mientras que *Paralichthys californicus* se estableció con tamaño pequeño, utilizó las bahías como áreas de cria, y demoró la maduración.

INTRODUCTION

Flatfishes (order Pleuronectiformes) have complex life histories of pelagic eggs and larvae and demersal adults. Larvae are symmetrical, but transform into asymmetrical juveniles (both eyes on one side of the head) that settle to the bottom. The duration of the pelagic larval stage and the size at transformation vary among flatfishes, but the general trend is toward longer pelagic larval stage and larger settlement size with increasing depth of adult habitat (Moser 1981).

Interspecific differences in morphology among flatfishes result in interspecific differences in soft-bottom resource use. For example, flatfishes can be divided into two groups: species that have large, symmetrical mouths and feed on fish and large crustaceans living on or above the bottom, and species that have small, asymmetrical mouths and feed on worms and small crustaceans living on or in the substrate (Allen 1982).

Off southern California, Pleuronectiformes are the most abundant soft-bottom fishes caught in otter trawls (Allen 1982). Reports of bottom-trawl surveys off southern California lack information on size-specific abundance of soft-bottom species (Allen 1982; DeMartini and Allen 1984; Love et al. 1986). Most of these surveys sampled depths greater than 12 m.

The objective of this paper is to describe the size-specific distribution and abundance of the seven most abundant flatfish species found along the shallow open coast and bay habitats of southern California. The organization and dynamics of the flatfish assemblage will be discussed in light of these findings.

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MATERIALS AND METHODS

Monthly collections were taken on the open coast and in bays from September 1986 to September 1988, and followed a stratified random design (for details see Kramer 1990a). Four blocks were sampled that represented 40 n.mi. of the open coast between Mission Bay and San Onofre: San Onofre, offshore of Agua Hedionda Lagoon, Torrey Pines, and Mission Beach (figure 1).

The two bays sampled were Mission Bay and Agua Hedionda Lagoon. Each was divided into blocks of similar habitat (five blocks in Mission Bay, three in Agua Hedionda Lagoon) (Kramer 1990a). Three to four randomly selected isobaths were sampled within three depth strata for each block. On the open coast, the three depth strata were from about 5 m (near the first breaker line) to 8 m, 9 to 11 m, and 12 to 14 m. In bays, strata ranged from "shoreline" (<1 m) to "open water" strata of 1–2-m and 2–4-m depths. San Diego Bay was sampled in June and July 1988, by means of a similar design but with 12 blocks (figure 1). The area of each habitat was computed from navigational charts (Kramer 1990a).

Gear consisted of two beam trawls with mouth openings of 1.6 and 1.0 m, and a 1-by-6-m beach seine. Gear was lined or made of 3-mm mesh netting. A meter wheel was mounted on the trawls to track distance traveled along the bottom, and to allow estimation of the area swept by each trawl (Krygier and Horton 1975).

The 1.6-m beam trawl was fished from a small (15-m) vessel, and the 1.0-m beam trawl was fished from a skiff (5 m) or pulled by hand in shallow water (<1 m). The beach seine and 1.0-m beam trawl were pulled parallel to shore at depths <1 m, for a distance of 20–50 m.

All flatfishes taken in trawls and seines were measured (standard length [SL] in mm), and fish were selected at random and frozen for later analysis in the laboratory (Kramer 1990b). At the laboratory, each fish was thawed, measured (SL in mm), and weighed (wet weight in g). Biomass was estimated by converting standard lengths into wet weight using allometric equations describing the relationship between standard length and wet weight (Kramer 1990b).

Mean density (no./ha) was determined for flatfish species and their length classes by season, location, and depth. Five length classes were used for speckled sanddab: SL ≤ 40 mm, 41–60 mm, 61–80 mm, 81–100 mm, and >100 mm. Six 50-mm length classes were used for California halibut: SL ≤ 50 mm, 51–100 mm, 101–150, 151–200, 201–250, and >250 mm. For the remaining species, five 50-mm length classes were used: SL ≤ 50 mm, 51–100, 101–150, 151–200, and >200 mm. No corrections were made for bias due to gear type.

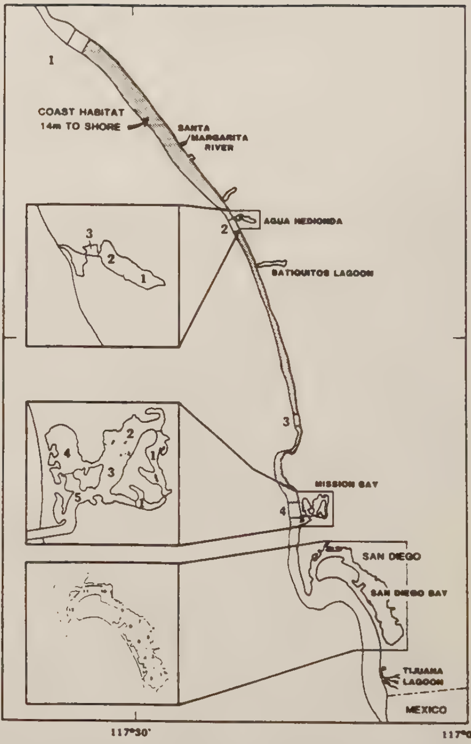

Figure 1. Map of location of sampling blocks. Open-coast blocks are (*1*) San Onofre, (*2*) adjacent to Agua Hedionda Lagoon, (*3*) Torrey Pines, and (*4*) Mission Beach. The two bays routinely sampled were Agua Hedionda Lagoon and Mission Bay, with sampling in San Diego Bay in June–July 1988.

Seasonality of settlement was determined by the temporal pattern of settlement. For each species, "newly settled" individuals were classified by length; maximum was 10 mm above the minimum estimated transformation length in published literature (Ahlstrom et al. 1984).

Analysis of variance (ANOVA) was used to describe the variability in density by length class (density in no./ha) with respect to location (four open-coast blocks and two bays), season (fall 1986 through summer 1988), and depth (<5 m, 5–8 m, 9–11 m, 12–14 m). An accepted significance level of $P \leq 0.05$ was used for all analyses except where noted. Abundance was determined by multiplying the mean density for each habitat by the area of each habitat. Abundance estimates were summed for open coast and bay habitats.

RESULTS

Thirteen flatfish species representing three families were captured. Seven species belonged to the family Paralichthyidae (Hensley and Ahlstrom 1984): California halibut, *Paralichthys californicus*; fantail sole, *Xystreurys liolepis*; speckled sanddab, *Citharichthys stigmaeus*; Pacific sanddab, *Citharichthys sordidus*; longfin sanddab, *Citharichthys xanthostigma*; gulf sanddab, *Citharichthys fragilis*; and bigmouth sole, *Hippoglossina stomata*. Five species were of the family Pleuronectidae: spotted turbot, *Pleuronichthys ritteri*; hornyhead turbot, *Pleuronichthys verticalis*; curlfin turbot, *Pleuronichthys decurrens*; English sole, *Parophrys vetulus*; and the diamond turbot, *Hypsopsetta guttulata*. California tonguefish, *Symphurus atricauda*, was the only member of the family Cynoglossidae.

The total number of flatfishes caught was 32,546; seven of the thirteen species accounted for >99% of the catch (California halibut, speckled sanddab, spotted turbot, hornyhead turbot, fantail sole, diamond turbot, and California tonguefish). Paralichthyidae represented 91.9% of the catch, followed by by Pleuronectidae with 7.7%, and Cynoglossidae with 0.4%. Three species of paralichthyid flatfishes accounted for 91.89% of the catch (California halibut, speckled sanddab, and fantail sole), and three species of pleuronectid flatfishes accounted for 6.9% (spotted, hornyhead, and diamond turbots).

Total biomass of the seven most abundant flatfish species was estimated at 662 kg. Paralichthyidae represented 68.3% of the total biomass, followed by Pleuronectidae with 31.3%, and Cynoglossidae with 0.4%.

The sampling design covered only a portion of the depth range of many species, and the beam trawls undersampled California halibut and probably other flatfishes >250 mm SL relative to otter trawls (Kramer 1990a). For example, speckled sanddab is small (maximum length = 144 mm SL) and is probably sampled effectively by the gear; however, the species is abundant at greater bottom depths than those sampled (depths of maximum abundance 5 to 40 m; figure 2). Thus abundance estimates did not fully represent the entire population of any species.

Density, abundance, and distribution of tonguefish were poorly estimated in this study because of their diurnal behavior. Tonguefish is nocturnally active: it remains buried in the sand or mud during the day and feeds at night. Tonguefish is the only flatfish in southern California coastal waters that has diel behavior that affects availability to trawling (DeMartini and Allen 1984).

Size Range (Figure 2)

Speckled sanddab was the smallest flatfish species captured (5–135 mm SL), followed by California tonguefish (21–208 mm). Spotted turbot (7.5–237 mm), diamond turbot (7–266 mm), and hornyhead turbot (10–265 mm) were similar in size: spotted turbot and diamond turbot have a maximum recorded length of 375 mm SL, whereas hornyhead turbot has a maximum recorded length of 290 mm (Miller and Lea 1972).

The largest flatfishes were California halibut and fantail sole. Fantail sole ranged from 7.5 to 340 mm SL, but has a maximum recorded length of 423 mm (Miller and Lea 1972). California halibut was the largest flatfish taken in this survey; standard length ranged from 6.1 to 600 mm, which is considerably less than the maximum recorded length of about 1,300 mm (Miller and Lea 1972).

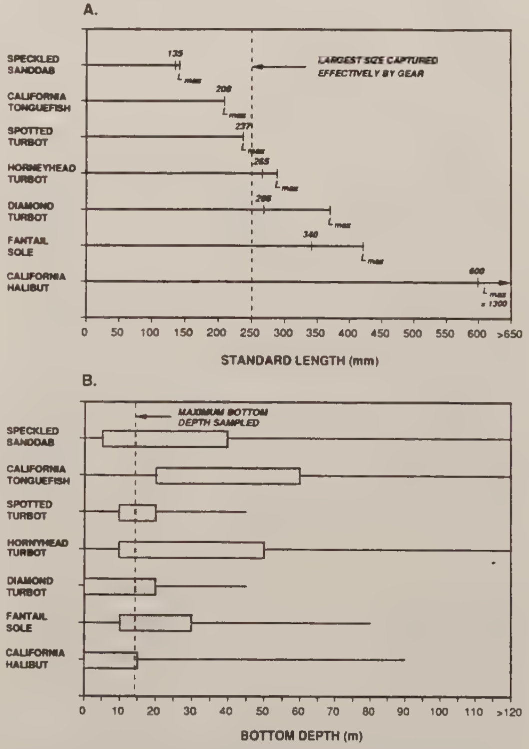

Figure 2. *A*, Maximum standard length and range captured effectively by sampling gear. *B*, Maximum depth, depths of maximum abundance, and outer bound of sampling depth. Lengths and depths obtained from literature (Ford 1965; Miller and Lea 1972; Allen 1982; DeMartini and Allen 1984; Love et al. 1986).

Catch Statistics (Figure 3)

Numbers captured. Speckled sanddab was the most abundant flatfish (25,298 fish), and represented 78.6% of the flatfish catch. Distribution of speckled sanddab varied in both space and time; 45% were caught at Torrey Pines, and 27.1% were caught in spring 1988. Almost all (99.6%) speckled sanddab were found on the open coast, and most were caught deeper than 10 m.

California halibut ranked second in number captured (4,085), and represented 12.6% of the flatfish catch. Most halibut were caught in bays: 60.2% came from Mission Bay and Agua Hedionda Lagoon, and 46.2% from Mission Bay alone. The total number of halibut captured decreased with depth.

Spotted turbot followed California halibut (956), and represented 2.9% of the flatfish catch. Greatest numbers (36.3%) were caught at Mission Beach. Most spotted turbot were caught on the open coast (83.9%); some were taken in the outer areas of Mission Bay.

Diamond turbot was fourth in number taken (848), representing 2.6% of the flatfish catch. Most diamond turbot were caught in bays—43% in Mission Bay and 40% in Agua Hedionda Lagoon. The number captured decreased with depth.

Hornyhead turbot ranked fifth in number (423), and represented 1.3% of the flatfish catch. Most hornyhead turbot (33.3%) were caught at Torrey Pines. Only four were caught in bays (0.9%), all in the entrance channel to Mission Bay. Hornyhead turbot increased in abundance with depth.

Fantail sole ranked seventh in numerical abundance (228), and represented 0.7% of the flatfish catch. Most (99.1%) fantail sole came from the open coast, and 45% were taken offshore of Agua Hedionda Lagoon.

California tonguefish ranked seventh in numerical abundance (129), and represented 0.4% of the flatfish catch. Mission Bay yielded 48% of the California tonguefish catch.

Biomass. California halibut had the highest biomass at 307.0 kg, or 46.4% of the flatfish biomass. Highest biomass was on the open coast offshore of Agua Hedionda Lagoon (67.3 kg, or 21.9% of the halibut biomass, and 10.2% of the flatfish biomass). Total biomass increased with depth to 11 m, and then declined.

Spotted turbot was second highest, at 117.5 kg, or 17.8% of the flatfish biomass. Highest biomass was at Mission Beach (46 kg, or 39.2%), followed by Carlsbad (29.4 kg, or 25%). Biomass was highest in the 9–11-m depth stratum on the open coast.

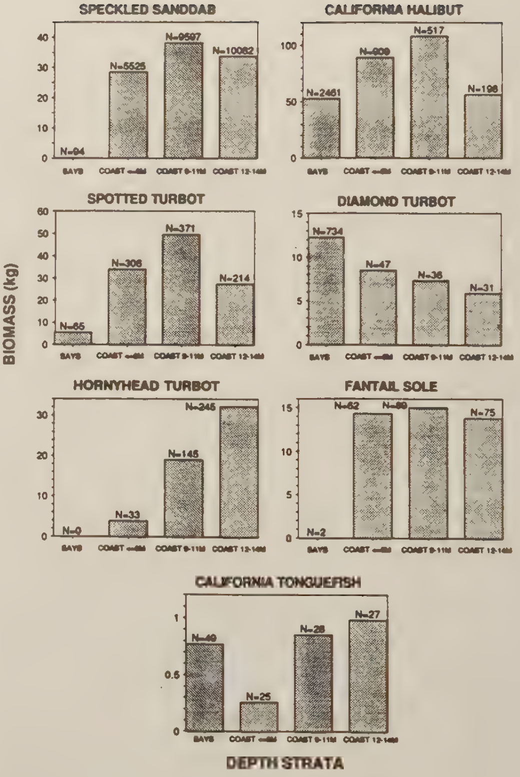

Figure 3. Total biomass and number captured by depth stratum for seven flatfish species.

Biomass of speckled sanddab was 101.0 kg, and ranked third (15.3%) in flatfish biomass, followed by hornyhead turbot with 55.4 kg, or 8.4% of flatfish biomass. Hornyhead turbot biomass increased with increasing bottom depth.

Fantail sole ranked fifth in biomass, with a total of 43.3 kg, or 6.6% of the flatfish biomass. Biomass was relatively constant across all open-coast depth strata, and ranged from 14 to 16 kg.

Diamond turbot had the sixth highest total biomass, at 34.3 kg, or 5.2% of the total biomass. Biomass was highest in bays (12.5 kg, or 36.5%), and decreased with depth.

Biomass of tonguefish was the lowest, at 2.9 kg, or 0.5% of the flatfish biomass. Greatest biomass was in Mission Bay (1.0 kg, or 35%). Biomass on the open coast increased with depth.

Variations in Density[2]

Depth. Density of speckled sanddab and hornyhead turbot varied significantly with depth (F = 387.1, df = 3, 3516, $P < 0.01$; and F = 52.7, df = 3, 3516, $P < 0.01$, respectively), and increased with depth. Speckled sanddab density increased from a mean of 272.5/ha (SE = 17.5) in the shallowest open coast stratum (5–8 m) to 630.8/ha (SE = 50.7) in the deep stratum (12–14 m). Hornyhead turbot increased from 1.24/ha (SE = 0.36) in the shallowest open-coast stratum to 16.2/ha (SE = 1.36) in the deepest stratum.

Density of California halibut also differed significantly with depth (F = 37.6, df = 3, 3516, $P < 0.01$). The smallest length class ($\leq$50 mm) was most dense in bays (mean = 46.7, SE = 4.5), and decreased with depth on the open coast (shallowest coastal stratum mean = 11.7, SE = 2.7; deepest coastal stratum mean = 1.9, SE = 1.0). Density of the larger classes increased with depth; the largest class (>250 mm) was least dense in the bays (mean = 0.5, SE = 0.1) and most dense in the deepest coastal stratum (mean = 5.7, SE = 0.6). Halibut <150 mm were found primarily in the bays; larger halibut were found on the open coast.

Density of spotted turbot differed significantly with depth (F = 12.9, df = 3, 3516, $P < 0.01$). Spotted turbot was most dense in the shallow and mid-depth strata (5–11 m) on the open coast ($\text{mean}_{\text{shallow}}$ = 20.7/ha, SE = 1.9; $\text{mean}_{\text{middle}}$ = 21.5/ha, SE = 1.5), with the lowest open-coast density in the deep stratum ($\text{mean}_{\text{deep}}$ = 14.5, SE = 1.1). Lowest densities were found in bays, with a mean of 2.1/ha (SE = 0.4). Spotted turbot were found in shallow coastal habitats, but not in bays (figure 4).

Density of tonguefish in the 151–200-m class varied significantly with depth (F = 5.7, df = 3, 3516, $P < 0.01$). However, the smallest (<50 mm) and the largest (151–200 mm) tonguefish were caught in deeper coastal waters (9 m), with intermediate length classes in shallow coastal water (<7 m) and in the bays (figure 4).

Density of fantail sole did not vary significantly with depth for any of the length classes (F = 2.2, df = 3, 3516, $P > 0.05$).

Location. Densities of California halibut and diamond turbot differed significantly with location (F = 33.0, df = 5, 3516, $P < 0.01$; and F = 47.0, df = 5, 3516, $P < 0.01$, respectively). These fish were most dense in bays, where there were seasonally high concentrations of juveniles. The highest density of diamond turbot occurred during the period of peak settlement of juveniles, with a maximum of 864/ha (SE = 248) in Agua Hedionda Lagoon in winter 1987, and 51.8/ha (SE = 20) in Mission Bay in spring 1987. Halibut was also most dense during settlement of juveniles, with a maximum of 188/ha (SE = 15.7) in Mission Bay in spring 1987, and 797/ha (SE = 410) in Agua Hedionda Lagoon in winter 1987.

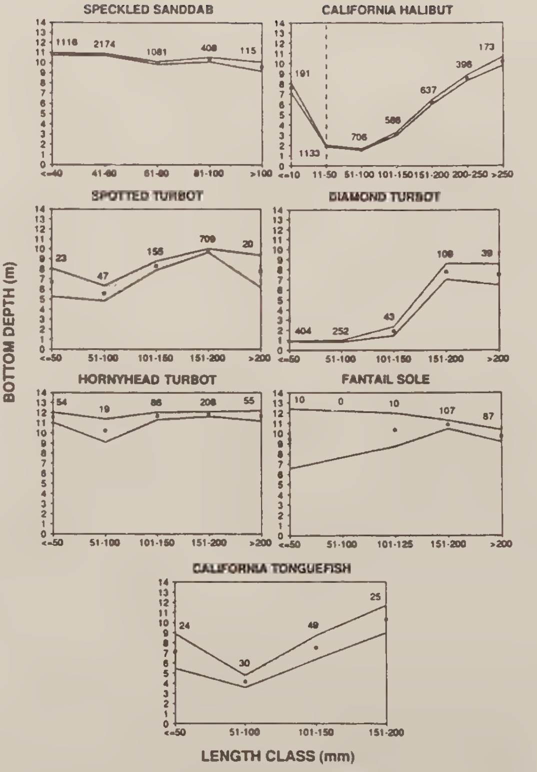

Figure 4. Mean bottom depth of standard length classes for seven flatfish species.

There were more California halibut and diamond turbot at open coast locations adjacent to bays than in areas far from bays. Density in bays ranged from 36.5/ha (SE = 2.9) offshore of Agua Hedionda Lagoon to 12.1/ha (SE = 1.3) at San Onofre. Maximum coastal densities of diamond turbot were at Mission Beach, ranging from 1.3/ha (SE = 0.85) in fall 1986 to 12.7/ha (SE = 3.6) in fall 1987. Density of diamond turbot in the >250-mm class did not vary significantly with location (F = 0.6, df = 5, 3516, P = 0.71).

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[2] Tables of density for each species by sample block, quarter, and length class are available in Kramer 1990b.

TABLE 1
Key Life-History Characteristics of Inshore Flatfishes

A. Juveniles

Species	Size at settlement	Settlement location*	Settlement depth			Ontogenetic distribution
			Mean	SD	*N*	
California halibut	≤17	B, C	5.05	3.67	398	Yes
Diamond turbot	≤14	B	1.25	0.46	51	Yes
Speckled sanddab	≤35	C, B	11.02	2.25	773	No
Fantail sole	≤17	C	6.35	5.91	4	No
Hornyhead turbot	≤17	C	8.84	2.54	5	No
Spotted turbot	≤16	C	9.19	4.35	4	No
California tonguefish	≤29	C, B	11.37	1.20	10	?

B. Adults

	Size at 1st maturity (a)	Maximum SL (mm)	Depth distribution	Major prey	Season of spawning†
California halibut	300+	1274	≤15 (d,e,j,k)	Anchovies (b,e)	W,Sp,Su
Diamond turbot	160	373	≤20 (d,j,k)	Polychaetes (c)	W,F
Speckled sanddab	70	144	5–40 (d,e,j,k)	Mysids (d,e)	Sp,Su,F (g)
Fantail sole	160	423	10–30 (d,e,j,k)	Crabs (e)	Su,F
Hornyhead turbot	140	290	10–50 (d,e,j,k)	Polychaetes (e,f)	W,Sp,Su?,F? (h)
Spotted turbot	140	237	10–20 (d,j,k)	Anemones (e,f)	Sp,Su,F?,W?
California tonguefish	120	208	20–60 (d,e,j,k)	Amphipods (e)	Su,F? (i)

(a) Miller and Lea 1972; (b) Plummer et al. 1983; (c) Lane 1975; (d) Ford 1965; (e) Allen 1982; (f) Luckinbill 1969; (g) Goldberg 1987; (h) Goldberg 1982a; (i) Goldberg 1981; (j) Love et al. 1986; (k) DeMartini and Allen 1984.
*B = bays; C = coast
†W = winter; Sp = spring; Su = summer; F = fall

Diego Bay. High abundance there suggests that the bay may be an optimal habitat for spotted turbot and tonguefish, or that it is an area of increased susceptibility to capture with the beam trawl. The entrance is dredged to about 15 m and has a sandy bottom similar to the open coast. The channel is protected from large swells, but is influenced by tidal currents. The bottom was populated with sea pens, *Stylatula* sp., and was the only location where dense stands of sea pens were found. *Stylatula* has been found in the stomachs of spotted turbot, and may be an important food (Ford 1965).

Fantail sole, hornyhead turbot, speckled sanddab, and English sole did not depend on shallow-water nursery habitats. Newly settled fantail sole and hornyhead turbot were caught from March to September 1989, whereas speckled sanddab settled throughout both 1989 and 1990 but were caught in greatest numbers from March to September 1989 (figure 5).

Juvenile English sole were found only on the open coast, although they use bays as nursery areas in northern California, Oregon, and Washington (Toole 1980; Krygier and Pearcy 1986; Rogers et al. 1988). The English sole settled on the open coast between April and September, at about the same time as halibut, but in deeper water and at a larger size (figure 5; table 1).

The seasonal spawning pattern is winter and spring for species using bays and the shallow open coast as nursery areas (diamond turbot, California halibut). But species that settle in deeper waters of the open coast spawn throughout the entire year or in other seasons (table 1).

Annual Variation in Settlement

Variability in rates of settlement could be caused by differences in larval survival due to food availability or predation, variability in reproductive effort and abundance of adults, or variability in oceanographic conditions influencing the transport of larvae to the nearshore. Newly settled and small juveniles of all species were more abundant in 1988 than 1987, suggesting that the factors influencing settlement success affect the entire nearshore environment. Ford (1965) also found considerable variability in population estimates for speckled sanddab in 1962 and 1963, which suggests that there is high interannual variability in speckled sanddab abundance.

Spatial patterns in settlement were also evident, with most of the coastal settlement of speckled sanddab and California halibut at Torrey Pines in 1988. It seems unlikely that increased egg production would account for the spatial and temporal settlement patterns for all species; therefore the increased settle-small juvenile diamond turbot use bays as nursery areas.

Size and Season of Settlement (Figure 5)

Diamond turbot larvae are the smallest of the flatfishes at transformation, ranging from 4.4 to 8.8 mm SL (Ahlstrom et al. 1984). Juveniles of ≤14 mm were considered "newly settled"; 51 newly settled juveniles were caught—45 (88%) in winter 1988. All settlement occurred in bays, in the blocks farthest from the entrances.

Length at transformation of California halibut ranges from 7.5 to 9.4 mm SL (Ahlstrom et al. 1984). Juveniles ≤17 mm were considered newly settled. A total of 398 newly settled halibut was caught from February to May 1987 and from January to September 1988. Most newly settled halibut (271) were caught on the open coast in 1988, with over 50% (144) at Torrey Pines, followed by offshore of Agua Hedionda Lagoon (41, or 15%). Fewer newly settled halibut (127) were caught in 1987, and nearly all (124, or 97.6%) were in the bays. Of these, most settled in the blocks between the entrance and the middle of the bays.

Speckled sanddab larvae are the largest of the flatfish group at transformation, ranging in length from 24 to 35.5 mm SL (Ahlstrom et al. 1984). Juveniles of ≤35 mm were considered newly settled, and 7,456 newly settled speckled sanddab were caught in the survey. Although some settlement occurred throughout both years, peak settlement was between May and October in 1987, and from February until the end of the sampling program in September 1988. Speckled sanddab settlement was greatest in 1988, with over 50% at Torrey Pines (*n* = 2,920), followed by the open coast offshore of Agua Hedionda Lagoon (*n* = 1,614).

Newly settled juveniles of the remaining species were relatively rare. Spotted turbot, hornyhead turbot, and fantail sole all transform at a small size (Ahlstrom et al. 1984), and were considered newly settled at ≤17 mm SL. Only 4 newly settled spotted turbot were caught, in May and June 1988. Five newly settled hornyhead turbot were captured in August 1988 on the open coast offshore of Agua Hedionda Lagoon and at Torrey Pines. From March through September 1988, 4 newly settled fantail sole were captured: 2 in Mission Bay, and 2 on the open coast at Torrey Pines.

California tonguefish transform at a relatively large size (19–24.2 mm; Ahlstrom et al. 1984), with juveniles of ≤ 29 mm considered newly settled. Ten newly settled tonguefish were caught on the open coast at depths ≥9 m: 7 in fall 1986, and 3 from December 1987 through March 1988.

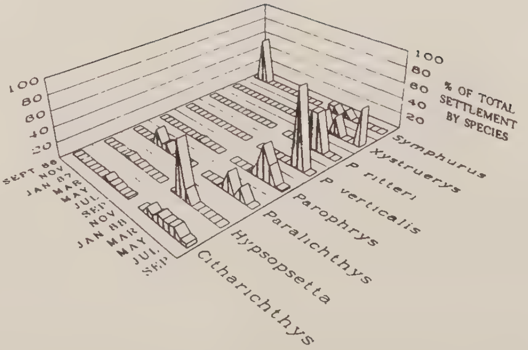

Figure 5. Settlement seasonality (percentage of newly settled fish by species each month) for eight flatfishes: speckled sanddab, *Citharichthys stigmaeus* (*n* = 7,456); California halibut, *Paralichthys californicus* (*n* = 398); spotted turbot, *Pleuronichthys ritteri* (*n* = 4); diamond turbot, *Hypsopsetta guttulata* (*n* = 51); hornyhead turbot, *Pleuronichthys verticalis* (*n* = 5); fantail sole, *Xystreurys liolepis* (*n* = 4); California tonguefish, *Symphurus atricauda* (*n* = 10); and English sole, *Parophrys vetulus* (*n* = 159).

Abundance Estimates

Speckled sanddab. Speckled sanddab was most abundant in 1988 (figure 6). Total abundance estimated for both spring and summer 1988 by location was: San Onofre, 1,562,539 (SE = 183,131), Agua Hedionda, 833,415 (SE = 71,099), Torrey Pines, 1,293,550 (SE = 154,833), and Mission Beach, 1,036,291 (SE = 98,419). Estimated abundance for spring and summer 1987 was significantly less than that for 1988. For example, abundance at Torrey Pines for both spring and summer 1987 was 372,317 (SE = 69,400), which is about one quarter of the abundance in 1988.

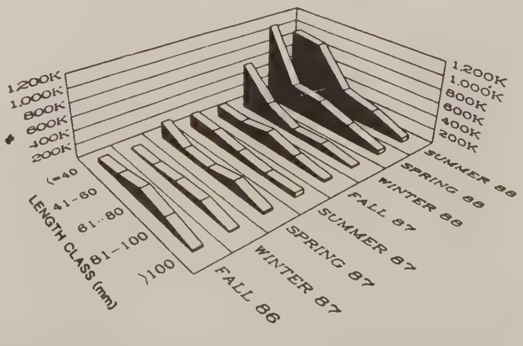

Figure 6. Total abundance of speckled sanddab estimated by season for the open coast.

California halibut. Nearly all halibut in the 51–100-mm length class were found in the bays, whereas most of the halibut in the 201–250-mm class were found on the open coast (figure 7).

In 1987, 50-mm juveniles were more abundant in bays than in 1988; conversely, they were more abundant on the coast in 1988 than in 1987. Abundance of halibut <50-mm summed over all habitats for both years differed significantly, being higher in 1987 than 1988 (n_{1987} = 227,055, SE = 17,623; n_{1988} = 155,407, SE = 16,966). Although settlement occurred on the open coast in 1988, juvenile halibut in the 51–100-mm length class were not found on the open coast.

Spotted turbot. Lack of small spotted turbot on the shallow open coast suggests that they did not use shallow habitats as a nursery area (figure 8). Density of spotted turbot in all except the 150–200-mm class appears to be underestimated or incompletely sampled.

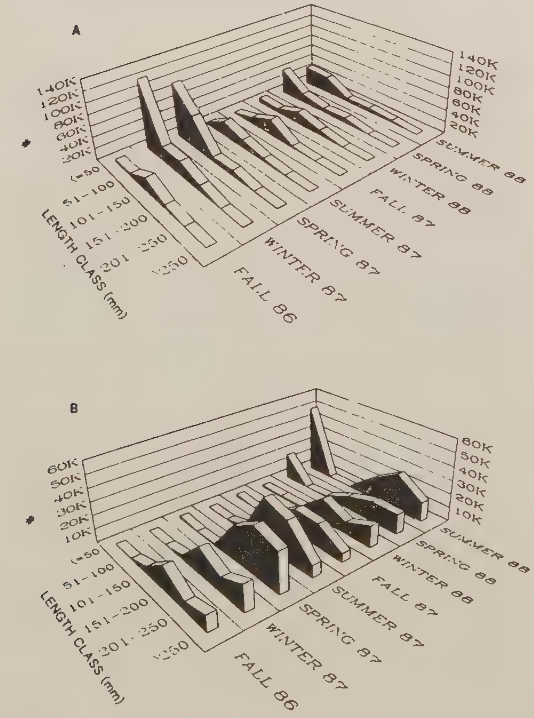

Figure 7. Total abundance of California halibut estimated by season for (*A*) bays and (*B*) open coast.

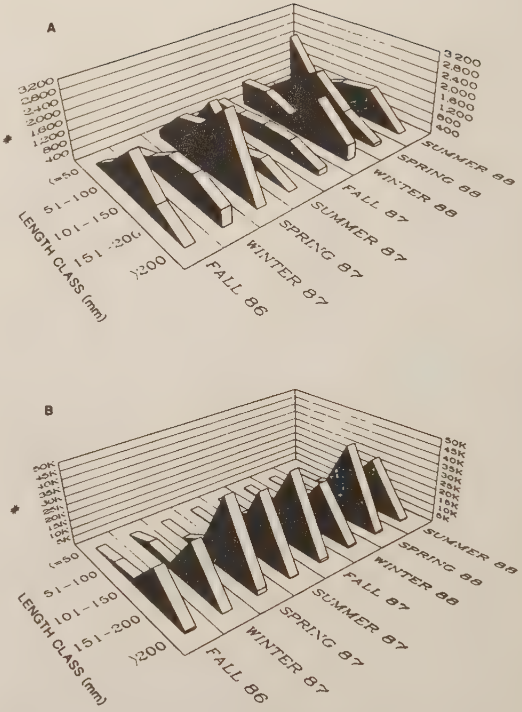

Figure 8. Total abundance of spotted turbot estimated by season for (*A*) Mission Bay and (*B*) open coast.

The most juvenile spotted turbot in the three smallest size classes (≤50, 51–100, and 101–150 mm) were found in the entrance channel to San Diego Bay during the June and July 1988 survey. Density of spotted turbot ≤50 mm ranged from 214 to 739/ha (mean = 473/ha, SE = 88), and was much higher than that at any other location.

Abundance of spotted turbot ≤50 mm at the San Diego Bay entrance (area = 600 ha) was 164,632 (SE = 53,433). Abundances of the 51–100, 101–150, and 151–200-mm length classes at the entrance to the bay were 12,432 (SE = 8,580), 35,640 (SE = 17,670), and 82,320 (SE = 26,452). These accumulations of small spotted turbot suggest that they may prefer the habitat at the entrance to San Diego Bay.

Total abundance of adults in the 151–200-mm class on the open coast ranged from a low of 23,000 (SE = 8,178) during fall 1986 to 45,264 (SE = 10,776) during spring 1988. Abundance was lower in the fall and winter than in the spring and summer (figure 8).

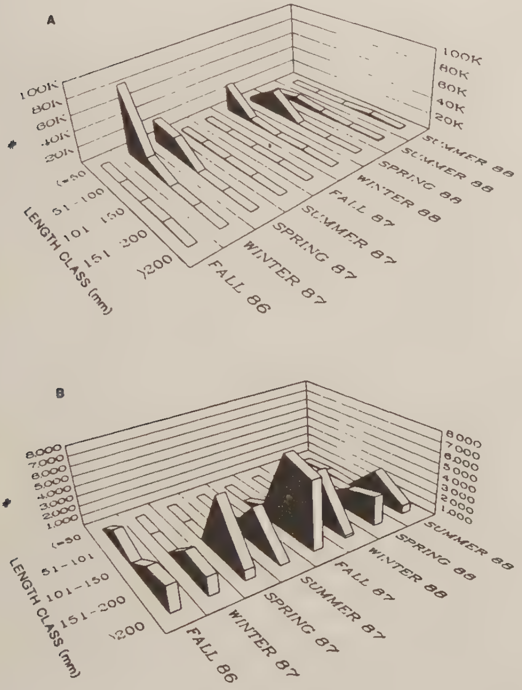

Figure 9. Total abundance of diamond turbot estimated by season for (*A*) bays and (*B*) open coast.

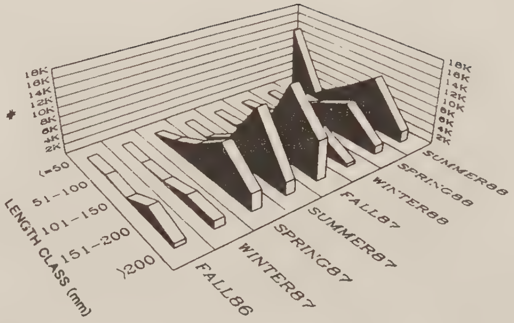

Figure 10. Total abundance of hornyhead turbot estimated by season for the open coast.

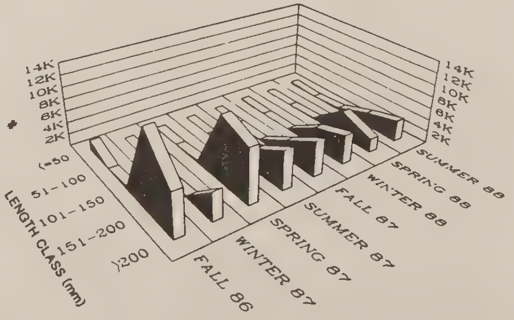

Figure 11. Total abundance of fantail sole estimated by season for the open coast.

Diamond turbot. The number of juvenile diamond turbot in bays appeared sufficient to support the adult population on the open coast (figure 9). Diamond turbot of 51–100 mm SL were most abundant in bays in spring, with 24,164 (SE = 554) in 1987 and 28,108 (SE = 580) in 1988. Maximum abundance of adults (151–200 mm) on the open coast was 7,632 (SE = 573) in fall 1987—considerably lower than the estimated production of juveniles from bays.

Hornyhead turbot. Hornyhead turbot ≤50 mm were most abundant on the open coast in summer 1988, with an estimated abundance of 13,853 (SE = 5,116) (figure 10). No small juveniles were caught on the open coast in 1987. Hornyhead turbot do not appear to use bays as nursery areas.

The 151–200-mm length class was most abundant, with greatest numbers in summer and fall of 1987: there were 14,006 (SE = 5,312) in summer and 16,210 (SE = 7,519) in fall on the open coast. Abundance was lower in winter, with 1,973 (SE = 1,973) in 1987 and 4,567 (SE = 2,151) in 1988. Winter lows and summer-fall peaks in abundance were consistent for both years of the survey, and may represent seasonal movements of adults across the shelf.

Fantail sole. Juvenile fantail sole <100 mm were rare or missing in collections, indicating that they did not use shallow habitats as nursery areas. Their nursery area is probably deeper than 15 m.

Abundance of adults on the open coast was comparable to abundance of diamond turbot and hornyhead turbot. Fantail sole in the 151–200-mm length class were most abundant in 1986 and 1987, with maximum seasonal abundance of 13,191 (SE = 1,161) in fall 1986, followed by 11,084 (SE = 791) in spring 1987 (figure 11). The abundance of >200-mm fantail sole ranged from 2,280 (SE = 360) in spring 1988 to 9,155 (SE = 755) in summer 1987. The fish appeared in the study in low numbers, without any obvious seasonal trends.

California tonguefish. Although density and abundance are underestimated, trends in the data are probably valid. Greatest density of tonguefish on the open coast was off Agua Hedionda Lagoon, with seasonal means ranging from 0 to 5.8/ha (SE = 2.35) for the 101–150-mm class and from 0 to 4.7/ha (SE = 1.79) for the 151–200-mm class (figure 12).

San Diego Bay had the highest density of tonguefish. Like spotted turbot, tonguefish were found primarily at the entrance of the bay (blocks 10–12, figure 1). The 51–100-mm class was most dense in the outermost block (block 12), with density ranging from 474 to 1,089/ha (mean = 705.9/ha, SE = 248.3). Density decreased farther into the bay, and was lower at block 10 (mean = 301.6/ha, SE = 143.5).

Estimated abundance of tonguefish in the 51–100-mm class from San Diego Bay was 368,303 (SE = 71,826). Tonguefish in the 51–100-mm class were caught in both Mission Bay and San Diego Bay, but not on the open coast.

Other Flatfish Species

Six additional flatfish species captured include *Citharichthys sordidus*, *C. xanthostigma*, *C. fragilis*, *Hippoglossina stomata*, *Pleuronichthys decurrens*, and *Parophrys vetulus*. Of the *Citharichthys* sp., *C. sordidus* and *C. fragilis* were rare, with only 6 fish captured along the open coast. Numbers captured and range in standard length were: *C. sordidus* (1; 21.5 mm) and *C. fragilis* (5; 18.3–24 mm). Longfin sanddab, *C. xanthostigma*, was more abundant: 96 were caught on the open coast. They ranged from 19.5 to 233 mm: 5 were <40 mm, and 91 were 129–233 mm. Only 1 *Hippoglossina stomata* (204 mm), and 8 *Pleuronichthys decurrens* (143–180 mm) were caught, all on the open coast.

English sole (*Parophrys vetulus*) was relatively uncommon: 262 were captured, and ranged from 10 to 295 mm. Most (159, or 61%) were newly settled, with standard length ≤30 mm (transformation length ca. 20 mm; Ahlstrom et al. 1984). Settlement occurred between May and September (figure 5). English sole were most abundant in summer 1988, when 134 fish, representing 51% of the English sole catch, were taken. Combined catch in spring and summer 1988 was 247, or 94% of the total catch of English sole.

There was no relationship between standard length and depth of capture; the mean bottom depth was 10.82 m for 50-mm fish (n = 207, SD = 2.48) and 10.81 m for 51–100-mm fish (n = 52, SD = 2.02). Only one English sole was taken from a bay, which suggests that in southern California, the open coast serves as a nursery.

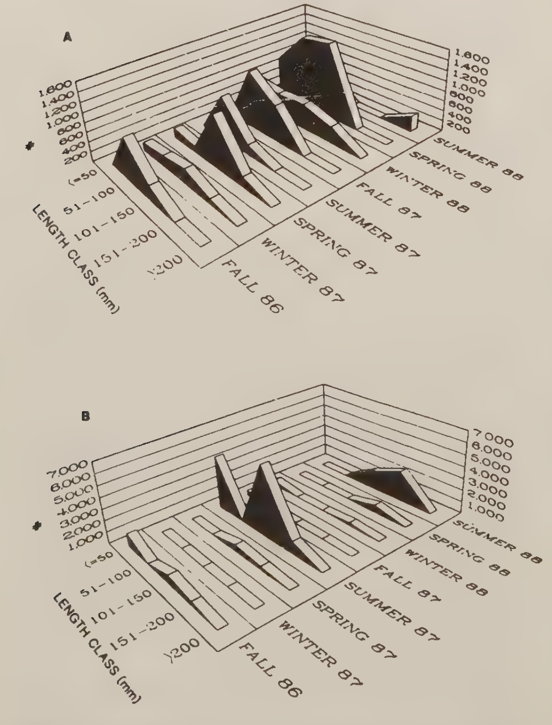

Figure 12. Total abundance of California tonguefish estimated by season for (*A*) Mission Bay and (*B*) open coast.

DISCUSSION

Season and Location of Settlement

Only California halibut and diamond turbot used bays as nursery areas, but timing and location of settlement were slightly different. Diamond turbot settled between January and March in back bays, whereas halibut settled primarily between March and September, either on the open coast or closer to the entrance in bays (figure 5). Both species settle at a small size (table 1) and spend little time in the plankton, perhaps as a strategy to decrease dispersal away from the nearshore habitats where adults spawn. Diamond turbot adults probably spawn in or near bays (Lane 1975), and halibut larvae are known to be distributed nearshore (Gruber et al. 1982; Barnett et al. 1984; Lavenberg et al. 1986; Moser and Watson 1990).

Tonguefish settled in the late fall and winter of both years, whereas spotted turbot settlement was observed only in May and June 1989 (figure 5). Spotted turbot and tonguefish both use nearshore nursery areas, probably including the entrance to San

Density of spotted turbot differed significantly with location (F = 66.0, df = 5, 3516, P = 0.01). There were more spotted turbot on the open coast than in bays, with highest density at Mission Beach (mean = 28.5/ha, SE = 2.0) and lowest at Agua Hedionda Lagoon (mean = 0.30/ha, SE = 0.30). The open coast offshore of Agua Hedionda Lagoon had the second highest density (mean = 17.8/ha, SE = 1.4), with lowest open-coast densities at the two locations farthest from bays ($\text{mean}_{\text{Torrey Pines}}$ = 9.1/ha, SE = 1.2; $\text{mean}_{\text{San Onofre}}$ = 7.2/ha, SE = 0.9).

Density of speckled sanddab also differed significantly between coastal locations (F = 138.4, df = 3, 1004, $P < 0.01$); highest density was at Torrey Pines (overall mean = 948.3/ha, SE = 73.0); the lowest was at San Onofre (mean = 180.9/ha, SE = 13.5). Highest density obtained in a single tow was 8,463/ha, or nearly 1/m^2, and was taken in the deep stratum at Torrey Pines in summer 1988.

Density of hornyhead turbot, fantail sole, and California tonguefish also varied significantly with location, except for the following rare length classes: hornyhead turbot 51–100 mm; fantail sole juveniles ≤50 mm; and tonguefish 51–100 mm. Like speckled sanddab, hornyhead turbot was most dense on the open coast at Torrey Pines (mean density = 12.7/ha, SE = 1.42), and least at San Onofre (mean = 1.65/ha, SE = 0.38). The highest density of >200-mm fantail sole was also at Torrey Pines, with a mean of 2.58/ha (SE = 0.5). Tonguefish was most dense on the open coast offshore of Agua Hedionda Lagoon (mean = 3.1/ha, SE = 0.62), and least at Torrey Pines (mean = 0.24/ha, SE = 0.17).

Seasonality. Density of speckled sanddab, California halibut, diamond turbot, and hornyhead turbot varied significantly with season. Most of the seasonal variability was due to settlement of juveniles in the smallest length classes. Highest densities of speckled sanddab were obtained in spring and summer of 1988 (overall mean summer = 630.8, SE = 50.7). These high densities were due to large numbers of small juveniles in the ≤40-mm length class ($\text{mean}_{\text{spring}}$ = 495.2, SE = 41.9; $\text{mean}_{\text{summer}}$ = 405.3, SE = 49.3). Lowest density occurred in winter 1987 (overall mean = 102.5, SE = 11.4).

California halibut ≤50 mm had maximum densities in winter (mean = 63.9/ha, SE = 17.6) and spring of 1987 (mean = 96.9/ha, SE = 13.6), and in spring (mean 43.5/ha, SE = 6.2) and summer 1988 (mean = 34.0/ha, SE = 5.1).

Density differed significantly with season only for diamond turbot ≤50-mm, and did not differ significantly for the larger classes ($P_{\text{SL101–150 mm}}$ = 0.07, $P_{\text{SL151–200 mm}}$ = 0.75, $P_{\text{SL201–250 mm}}$ = 0.52, and $P_{\text{SL>250 mm}}$ = 0.39). Overall density was greatest in winter and spring, with mean densities ranging between 40.0/ha (SE = 8.75) in spring 1988 to 56.0/ha (SE = 13.4) in spring 1987. These peaks were due to settlement of juveniles.

Density of hornyhead turbot varied significantly with season for the ≤50-mm, 101–150-mm, and 151–200-mm length classes. The 51–100-mm and >200-mm classes did not differ significantly with season ($P_{\text{SL50–100 mm}}$ = 0.61, $P_{\text{SL>200 mm}}$ = 0.14), and were relatively rare, with maximum seasonal densities of 0.82/ha (SE = 0.55) for the 51–100-mm class and 2.47/ha (SE = 0.77) for the >200-mm class.

Density of large fantail sole (>151 mm) also differed significantly with respect to season. No fantail sole between 51 and 100 mm were caught. The fish were relatively uncommon, with overall densities ranging from 0.82/ha (SE = 0.23) in summer 1988 to 2.96/ha (SE = 0.53) in fall 1986.

There were no seasonal patterns in density of spotted turbot or California tonguefish. Spotted turbot ranged from a low mean density of 5.2/ha (SE = 1.1) in winter 1987 to a high of 11.9/ha (SE = 1.7) in spring 1987. The 151–200-mm class was most dense, regardless of season, and ranged from 2.7/ha (SE = 0.6) in winter 1987 to 7.8/ha (SE = 1.2) in spring 1987.

Relationship between Size and Depth (Figure 4)

There were insignificant or weak linear relationships between length and depth of capture for speckled sanddab, hornyhead turbot, fantail sole, tonguefish, and spotted turbot. California halibut length was positively correlated with depth, which suggests ontogenetic changes in depth distribution (Allen 1982; Plummer et al. 1983). The relationship between standard length (mm) and depth of capture (m) is:

$$\text{SL} = 14.87 * \text{DEPTH} + 48.19$$

(SE slope = 0.29, r^2 = 0.40, n = 3898). Transforming stages (SL ≤ 10 mm) were found on the open coast, with small juvenile halibut in bays at depths of 4 m and less, and larger halibut in the deeper coastal strata (>12 m).

Diamond turbot had a similar ontogenetic depth distribution to halibut, with the smallest individuals in the shallowest habitats. The linear regression describing standard length at depth of capture is:

$$\text{SL} = 15.12 * \text{DEPTH} + 41.27$$

(r^2 = 0.59, SE slope = 0.43, n = 848). Like halibut, ment may be due to differential larval mortality or transport on the coast.

Oceanographic conditions can lead to variability in the transport of larvae and juveniles to their prospective nearshore nursery habitats (Nelson et al. 1977; Mearns 1979; Cohen 1985; Boehlert and Mundy 1988). Currents in the Southern California Bight are characterized by minimal offshore Ekman transport and a gyral geostrophic flow pattern, resulting in minimal seaward dispersion (Owen 1980; Parrish et al. 1981).

Fish larvae can be transported onshore by internal waves, which occur when the water column is thermally stratified in spring, summer, and fall (Winant and Bratkovich 1981; Shanks 1983, 1988). Postflexion diamond turbot and California halibut are neustonic, and are distributed within 2–3 km of shore (Barnett et al. 1984; Moser and Watson 1990). Most of the nearshore coastal flatfishes have relatively short-lived planktonic larvae and settle at a small size, which may decrease the risk of dispersal to unfavorable areas.

Comparison of Life Histories

Size at settlement increases with settlement depth: diamond turbot settle at the smallest size in the shallowest habitats, and speckled sanddab settle at a larger size in deeper water (figure 13; table 1). Smaller size at settlement suggests shorter duration of pelagic stages and less dispersal, which may be advantageous for species using bays as nursery areas.

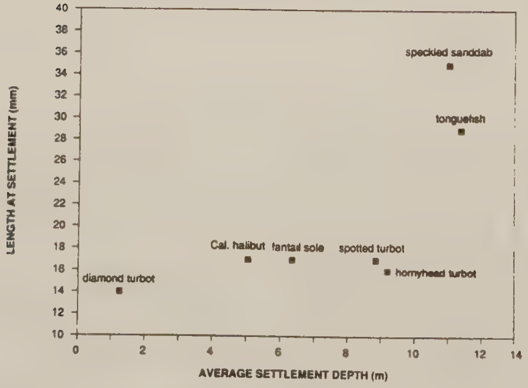

Figure 13. Size at settlement versus settlement depth.

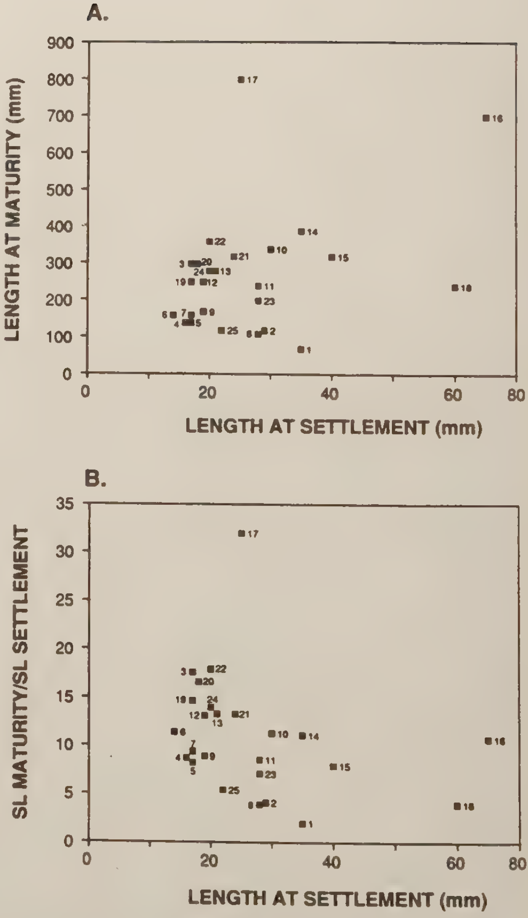

Figure 14. *A*, Length at maturity versus length at settlement for 25 species of flatfishes. *B*, Ratio of size at maturity/size at settlement versus length at settlement for 25 species of flatfishes. Length at settlement determined by adding 10 mm to smallest size at transformation (Ahlstrom et al. 1984). Size at maturity was obtained from Kramer 1990, or referenced below. Numbers in figure refer to fishes listed as follows: 1. *Citharichthys stigmaeus*; 2. *Symphurus atricauda*; 3. *Paralichthys californicus* (Haaker 1975); 4. *Pleuronichthys verticalis*; 5. *Pleuronichthys ritteri*; 6. *Hypsopsetta guttulata*; 7. *Xystreurys liolepis*; 8. *Citharichthys xanthostigma* (Goldberg 1982b); 9. *Hippoglossina stomata* (Goldberg 1982a); 10. *Parophrys vetulus* (Roff 1981); 11. *Microstomus kitt* (Roff 1981); 12. *Platichthys flesus* (Roff 1982); 13. *Pleuronectes platessa* (Roff 1982); 14. *Glyptocephalus cynoglossus* (Roff 1982); 15. *Microstomus pacificus* (Roff 1982); 16. *Reinhardtius hippoglossoides* (Roff 1982); 17. *Hippoglossus stenolepis* (Roff 1982); 18. *Glyptocephalus zachirus* (Hosie and Horton 1977); 19. *Pseudopleuronectes americanus* (Klein-MacPhee 1978); 20. *Platichthys stellatus* (Orcutt 1950); 21. *Limanda ferruginea* (Royce et al. 1959); 22. *Paralichthys dentatus* (Smith and Daiber 1977); 23. *Hippoglossoides platessoides* (Roff 1982); 24. *Limanda aspera* (Roff 1981); 25. *Limanda limanda* (Roff 1982).

After settlement, juveniles of some species allocate energy to growth, and others to reproduction. However, there is no apparent relationship between size at maturity and size at settlement (figure 14; table 1). Sizes at maturity and at settlement of 25 flatfish species indicate the range in these life history characteristics; speckled sanddab mature at the smallest size, and Pacific halibut (*Hippoglossus stenolepis*) at the largest (figure 14).

The ratio of size at maturity to size at settlement indicates the relative amount of energy put into growth or reproduction after settlement. This ratio is lowest for speckled sanddab; they settle and begin to reproduce soon afterwards, investing energy primarily in reproduction, not growth. The ratio is highest for Pacific halibut, which settle and then grow to a large size before reproducing.

Community Structure

Size-structured distribution patterns. Several species have size-structured distribution patterns, including California halibut and diamond turbot (figure 4). Separation of small juveniles from large adults may reduce the risk of cannibalism: large California halibut have been found with smaller halibut in their stomachs (Drawbridge 1990).

Juvenile halibut and diamond turbot both use bays as nursery areas, but there is little overlap in diet. Small diamond turbot eat primarily polychaetes and clam siphons, whereas small halibut eat crustaceans and small fish (Lane 1975; Haaker 1975; Peterson and Quammen 1982; Allen 1988; Drawbridge 1990). Potential juvenile competitors with diamond turbot include English sole, spotted turbot, and hornyhead turbot, but these three species do not use bays as nursery areas.

Speckled sanddab of all sizes are found together on the open coast. Risk of cannibalism is low, because sanddab settle at a size larger than the largest prey consumed by adults (most adult prey are 20 mm or shorter; Ford 1965). Species that do not segregate by size (including hornyhead turbot) may not have the risk of mortality due to cannibalism.

Habitat partitioning. Seven flatfish species inhabit shallow inshore habitats, but do not occur at the same size in the same habitats and do not eat the same prey (table 1). For example, halibut and speckled sanddab do not occur together over the same size range (20–130 mm SL); the halibut live in bays, speckled sanddab on the open coast (figure 4). Halibut's change in distribution suggests that movement from the bays to the open coast occurs when the fish are between 100 and 200 mm (Kramer 1990a). Larger halibut (>250 mm) are primarily piscivorous, and have been found with speckled sanddab in their stomachs (Ford 1965; Allen 1982; Plummer et al. 1983; Hobson and Chess 1986; Drawbridge 1990). Ford (1965) estimated that predation by California halibut could account for 78% of the total monthly mortality of speckled sanddab. Speckled sanddab may also prey upon newly settled halibut, which settle at a size small enough to be within the range (<20 mm) eaten by sanddab (Ford 1965).

Speckled sanddab and juvenile English sole both inhabit the open coast, and settle at about the same size (≤35 mm). They both eat copepods and mysids as small juveniles (<50 mm), but speckled sanddab continue to feed on mysids while English sole switch to a predominately polychaete diet by the time they reach 70 mm (Ford 1965; Toole 1980). Juvenile English sole and speckled sanddab have been found in Humboldt Bay, but not in the same habitats; English sole occur in the intertidal zone, speckled sanddab in deeper channels (Toole 1980).

California halibut and fantail sole are morphologically similar yet eat different prey. Larger juveniles (>200 mm) occur together on the open coast, but halibut eat fish and mysids, and fantail sole eat primarily decapods and other crustaceans (Ford 1965; Allen 1982; Plummer et al. 1983). Newly settled juveniles do not occur together; fantail sole settle in much deeper water (12–15 m; Moser and Watson 1990) than halibut.

Large juvenile and adult spotted turbot, hornyhead turbot, diamond turbot, and English sole occur together on the open coast, but have different diets: all of them eat polychaetes, but each eats different species. About 40% of the hornyhead turbot's diet by weight is the polychaete *Owenia fusiforma*, and 50% of spotted turbot's diet is anemones that are attached to the basal disc of the sand tube of polychaetes (Ford 1965; Luckinbill 1969). Diamond turbot also eat polychaetes, but clam siphons compose nearly 40% of the diet by weight (Ford 1965; Lane 1975; Peterson and Quammen 1982). English sole also eat polychaetes, but brittle stars compose 16% of the diet by volume (Ford 1965; Allen 1982). Although these species coexist, they partition the habitat by eating different prey.

Dietary overlap is probably greatest between newly settled and small juvenile stages of flatfish; food resources are partitioned during later juvenile and adult stages. Newly settled juveniles were found in different habitats, with very little overlap in distribution. Most species, including fantail sole, tonguefish, hornyhead turbot, and spotted turbot, probably settle at depths greater than those surveyed (>14 m). Speckled sanddab settled deeper than halibut, and both settled deeper than diamond turbot. Time of settlement also differed, with diamond turbot settling primarily in winter, halibut in spring, and speckled sanddab in late spring and summer (figure 5). Small juvenile stages (<50 mm) were also found in different habitats: diamond turbot in back bays, halibut in the middle sections of bays out to the open coast at depths <8 m, and speckled sanddab on the open coast at greater bottom depths (figure 4).

In conclusion, the flatfish species found in shallow-water habitats (≤14 m) do not occur together during early juvenile stages; they settle at different depths, have ontogenetic depth distributions, and settle at different times of the year. Older juveniles and adults partition the habitat by partitioning food resources and by living at different depths and locations. Life histories of nearshore flatfishes vary widely, from that of speckled sanddab, which settle at a large size on the open coast and mature rapidly, to that of California halibut, which settle at a small size, use bays as nurseries, and delay maturity.

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LITERATURE CITED

Ahlstrom, E. H., K. Amaoka, D. A. Hensley, H. G. Moser, and B. J. Sumida. 1984. Pleuronectiformes: development. *In* Ontogeny and systematics of fishes, H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr., and S. L. Richardson, eds. Spec. Publ. Am. Soc. Ichthyol. Herpet. No. 1, pp. 640–670.

Allen, L. G. 1988. Recruitment, distribution, and feeding habits of young-of-the-year California halibut (*Paralichthys californicus*) in the vicinity of Alamitos Bay—Long Beach Harbor, California, 1983–1985. Bull South. Calif. Acad. Sci. 87:19–30.

Allen, M. J. 1982. Functional structure of soft-bottom fish communities of the southern California shelf. Ph.D. thesis, Univ. Calif., San Diego, 577 pp.

Barnett, A. M., A. E. Jahn, P. D. Sertic, and W. Watson. 1984. Distribution of ichthyoplankton off San Onofre, California, and methods for sampling very shallow coastal waters. Fish. Bull., U.S. 82:92–111.

Boehlert, G. W., and B. C. Mundy. 1988. Roles of behavioral and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. Amer. Fish. Soc. Symp. 3:51–67.

Cowen, R. K. 1985. Large scale pattern of recruitment by the labrid, *Semicossyphus pulcher*: causes and implications. J. Mar. Res. 43:719–742.

DeMartini, E. E., and L. G. Allen. 1984. Diel variation in catch parameters for fishes sampled by a 7.6-m otter trawl in southern California coastal waters. Calif. Coop. Oceanic Fish. Invest. Rep. 15:119–134.

Drawbridge, M. A. 1990. Feeding relationships, feeding activity and substrate preference of juvenile California halibut, *Paralichthys californicus*, in coastal and bay habitats. M.S. thesis, San Diego State Univ. 214 pp.

Ford, R. E. 1965. Distribution, population dynamics and behavior of a bothid flatfish, *Citharichthys stigmaeus*. Ph.D. thesis, Univ. Calif., San Diego, 243 pp.

Goldberg, S. R. 1981. Seasonal spawning cycle of the California tonguefish, *Symphurus atricauda* (Cynoglossidae). Copeia 1981:472–473.

———. 1982a. Seasonal spawning cycles of two California flatfishes, *Pleuronichthys verticalis* (Pleuronectidae) and *Hippoglossina stomata* (Bothidae). Bull. Mar. Sci. 32:347–350.

———. 1982b. Seasonal spawning cycle of the longfin sanddab, *Citharichthys xanthostigma* (Bothidae). Fish. Bull., U.S. 80:906–907.

———. 1987. Seasonal spawning cycle of the speckled sanddab, *Citharichthys stigmaeus* (Bothidae). Bull. South. Calif. Acad. Sci. 86:164–166.

Gruber, D., E. H. Ahlstrom, and M. M. Mullin. 1982. Distribution of ichthyoplankton in the Southern California Bight. Calif. Coop. Oceanic Fish. Invest. Rep. 23:172–179.

Haaker, P. L. 1975. The biology of the California halibut, *Paralichthys californicus* (Ayres) in Anaheim Bay. *In* The marine resources of Anaheim Bay, E. D. Lane and C. W. Hill, eds. Calif. Dept. Fish Game, Fish. Bull. 165, pp. 137–151.

Hensley, D. A., and E. H. Ahlstrom. 1984. Pleuronectiformes: relationships. *In* Ontogeny and systematics of fishes, H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr., and S. L. Richardson, eds. Spec. Publ. Am. Soc. Ichthyol. Herpet. No. 1, pp. 670–687.

Hobson, E. S., and J. R. Chess. 1986. Relationships among fishes and their prey in a nearshore sand community off southern California. Environ. Biol. Fishes 17:201–226.

Hosie, M. J., and H. F. Horton. 1977. Biology of the rex sole, *Glyptocephalus zachirus*, in waters off Oregon. Fish. Bull., U.S. 75:51–60.

Klein-MacPhee, G. 1978. Synopsis of the biological data for the winter flounder, *Pseudopleuronectes americanus* (Walbaum). U.S. Dept. Comm. NOAA Tech. Rep. NMFS Circ. 414, 43 pp.

Kramer, S. H. 1990a. Distribution and abundance of juvenile California halibut (*Paralichthys californicus*) in shallow waters of San Diego County. Calif. Dept. Fish Game, Fish. Bull. 174.

———. 1990b. Habitat specificity and ontogenetic movements of juvenile California halibut, *Paralichthys californicus*, and other flatfishes in shallow waters of southern California. Ph.D. dissertation, Univ. Calif. San Diego, 266 pp. (also available as Southwest Fisheries Center Administrative Report LJ-90-22. National Marine Fisheries Service, Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038)

Krygier, E. E., and H. F. Horton. 1975. Distribution, reproduction, and growth of *Crangon nigricauda* and *Crangon franciscorum* in Yaquina Bay, Oregon. Northwest Sci. 49:216–240.

Krygier, E. E., and W. G. Pearcy. 1986. The role of estuarine and offshore nursery areas for young English sole, *Parophrys vetulus* Girard, of Oregon. Fish. Bull., U.S. 84:119–132.

Lane, E. D. 1975. Quantitative aspects of the life history of the diamond turbot, *Hypsopsetta guttulata* (Girard) in Anaheim Bay. *In* The marine resources of Anaheim Bay, E. D. Lane and C. W. Hill, eds. Calif. Dept. Fish Game, Fish. Bull. 165, pp. 153–173.

Lavenberg, R. J., G. E. McGowen, A. E. Jahn, J. H. Petersen, and T. C. Sciarrotta. 1986. Abundance of southern California nearshore ichthyoplankton: 1978–1984. Calif. Coop. Oceanic Fish. Invest. Rep. 27:53–64.

Love, M. S., J. S. Stephens, Jr., P. A. Morris, M. M. Singer, M. Sandhu, and T. C. Sciarrotta. 1986. Inshore soft substrata fishes in the Southern California Bight: an overview. Calif. Coop. Oceanic Fish. Invest. Rep. 27:84–106.

Luckinbill, L. S. 1969. Distribution and feeding relationships of the flatfishes *Pleuronichthys verticalis* and *P. ritteri*. M.S. thesis, Calif. State Univ., San Diego, 81 pp.

Mearns, A. J. 1979. Abundance, composition, and recruitment of nearshore fish assemblages on the southern California mainland shelf. Calif. Coop. Oceanic Fish. Invest. Rep. 20:111–119.

Miller, D. J., and R. N. Lea. 1972. Guide to the coastal marine fishes of California. Calif. Dept. Fish Game, Fish. Bull. 157, 235 pp.

Moser, H. G. 1981. Morphological and functional aspects of marine fish larvae. *In* Marine fish larvae. Morphology, ecology, and relation to fisheries, R. Lasker, ed. Univ. Wash. Press, Seattle, pp. 89–131.

Moser, H. G., and W. Watson. 1990. Distribution and abundance of early life history stages of the California halibut, *Paralichthys californicus*, and comparisons with the fantail sole, *Xystreurys liolepis*. Calif. Dept. Fish Game, Fish Bull. 174.

Nelson, W. R., M. C. Ingham, and W. E. Schaaf. 1977. Larval transport and year-class strength of Atlantic menhaden, *Brevoortia tyrannus*. Fish. Bull., U.S. 75:23–41.

Orcutt, H. G. 1950. The life history of the starry flounder *Platichthys stellatus* (Pallus). Calif. Dept. Fish Game, Fish. Bull. 78, 64 pp.

Owen, R. W. 1980. Eddies of the California Current system: physical and ecological characteristics. *In* The California islands: proceedings of a multidisciplinary symposium, D. M. Power, ed. Santa Barbara Museum of Natural History, Santa Barbara. pp. 237–263.

Parrish, R. H., C. S. Nelson, and A. Bakun. 1981. Transport mechanisms and reproductive success of fishes in the California Current. Biol. Oceanogr. 1:175–203.

Peterson, C. H., and M. L. Quammen. 1982. Siphon nipping: its importance to small fishes and its impact on growth of the bivalve *Protothaca staminea* (Conrad). J. Exp. Mar. Biol. Ecol. 63:249–268.

Plummer, K. M., E. E. DeMartini, and D. A. Roberts. 1983. The feeding habits and distribution of juvenile-small adult California halibut (*Paralichthys californicus*) in coastal waters off northern San Diego County. Calif. Coop. Oceanic Fish. Invest. Rep. 24:194–201.

Roff, D. A. 1981. Reproductive uncertainty and the evolution of iteroparity: Why don't flatfish put all their eggs in one basket? Can. J. Fish. Aquat. Sci. 38:968–977.

———. 1982. Reproductive strategies in flatfish: a first synthesis. Can. J. Fish. Aquat. Sci. 39:1686–1698.

Rogers, C. W., D. R. Gunderson, and D. A. Armstrong. 1988. Utilization of a Washington estuary by juvenile English sole, *Parophrys vetulus*. Fish. Bull., U.S. 86:823–831.

Royce, W. F., R. J. Butler, and E. D. Premetz. 1959. Decline of the yellowtail flounder (*Limanda ferruginea*) off New England. Fish. Bull., U.S. 146:169–267.

Shanks, A. L. 1983. Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. Mar. Ecol. Prog. Ser. 13:311–315.

———. 1988. Further support for the hypothesis that internal waves can cause shoreward transport of larval invertebrates and fish. Fish. Bull., U.S. 86:703–714.

Smith, R. W., and F. C. Daiber. 1977. Biology of the summer flounder, *Paralichthys dentatus*, in Delaware Bay. Fish. Bull., U.S. 75:823–830.

Toole, C. L. 1980. Intertidal recruitment and feeding in relation to optimal utilization of nursery areas by juvenile English sole (*Parophrys vetulus*: Pleuronectidae). Environ. Biol. Fishes 5:383–390.

Winant, C. D., and A. W. Bratkovich. 1981. Temperature and currents on the southern California shelf: a description of the variability. J. Phys. Oceanogr. 11:73–86.

Dynamics of Growth in the Early Life History of Shortbelly Rockfish *Sebastes jordani*

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Abstract.–The relationship between length and age of larval and juvenile shortbelly rockfish *Sebastes jordani*, determined from otolith microstructure, is complex. Models that assume size increases smoothly with age may not accurately describe growth in young-of-the-year rockfish. A segmented (piece-wise linear) regression model relating somatic and otolith size was used to back-calculate body length-at-age. The segments of this model coincide with different growth stanzas, which are separated by distinct life-history transitions. The composite function of this model, and a Gompertz curve relating otolith size and age, yielded a good fit to the back-calculated standard length-at-age data. Comparison of back-calculated with actual growth showed no evidence of size-selective mortality. The change in body length, as the number of otolith increments increased, was equal to the observed increase in length per day of a sequentially sampled cohort, validating the daily periodicity of the increments.

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Fishery Bulletin, U.S. 89:611–621 (1991).

The abundance of young-of-the-year fish, and ultimately the number that reach maturity, varies greatly among years. Much of this variation is unrelated to the size of the spawning stock, and understanding its causes remains a central focus of fisheries research (e.g., Hjort 1914, Sissenwine 1984, Rothschild 1986, Hollowed et al. 1987, Sinclair 1988). Mortality agents, such as starvation (Hjort 1914, Lasker 1975 and 1978, Houde 1977 and 1978, Theilacker 1978 and 1981, Grover and Olla 1986) and predation (Hunter 1981, Hunter and Kimbrell 1980, Sissenwine 1984, Bailey and Houde 1989), can operate strongly during early stages, and it is clear that mortality rates of young fish are higher than those experienced by older fish (Miller et al. 1988). Interannual variation in year-class strength can depend upon the rate of growth early in life (Houde 1987 and 1989, Underwood and Fairweather 1989). Under most conditions, the more rapidly fish grow through early, high-risk stages, the fewer die; small changes in growth rate can thus lead to a major change in recruitment (Houde 1987). Knowledge of the processes affecting growth during the early life history may help predict the occurrence of strong year-classes.

Numerous mathematical models have been developed to describe the growth process, including the Gompertz, von Bertalanffy, logistic, and exponential functions (Ricker 1979). Although these models usually perform well on adult stages, they commonly falter in predicting growth during the first few weeks of life. For example, Phillips (1964) used a von Bertalanffy function to model growth of shortbelly rockfish *Sebastes jordani*. The model predicted growth of adults well, but its accuracy deteriorated for young-of-the-year fish. Because somatic growth during early stages can be affected by abrupt physiological changes (e.g., flexion, juvenile transformation, and settlement), models that predict growth during this period should reflect (or describe) this complexity (Ricker 1979).

Rockfish (*Sebastes* spp.) are an important component of the west coast groundfish fishery (PFMC 1989). Growth rates of young rockfish have been estimated from linear models relating length to age (Boehlert 1981, Boehlert and Yoklavich 1983, Penney and Evans 1985, Haldorson and Richards 1987, Woodbury and Ralston 1991). Because most of these studies examined a narrow range of ages, linear models fit the data adequately. Although Penney and Evans (1985) showed that a linear model explained much of the variation in length during larval and juvenile stages of redfish, back-calculated growth rates varied systematically with age; growth rate was relatively slow for young larvae, more rapid for older larvae, and relatively slow again for juveniles. This suggests that it is possible to improve upon the linear model and provide a more accurate description of growth over the entire range of ages.

Since Pannella (1971) first discovered daily growth increments in otoliths, many researchers have used these microstructural features to study fish growth (see reviews in Campana and Neilson 1985, Jones 1986). By measuring the widths of daily increments within the otolith, and defining the relationship between standard length and otolith radius, one can back-calculate the somatic length of fish at any given age. This approach provides a powerful tool for estimating growth rates (e.g., Thorrold and Williams 1989). In this study, we used otolith microstructure to back-calculate the growth of larval and juvenile shortbelly rockfish *Sebastes jordani*. To do this we (1) determined when daily increments begin to form, (2) validated the daily periodicity of the increments, (3) developed a growth model for back-calculation, and (4) assessed the effects of size-selective mortality on back-calculated estimates of growth.

Table 1

Haul and collection data gathered during this study. On the first three cruises, larvae only were collected; on the May–June cruise, both larvae and juveniles were collected.

Dates (1989)	Research vessel	No. hauls	No. collected	No. aged
01 Feb.	RV *Ed Rickettes*	7	191	153
18 Feb.	RV *David Starr Jordan*	2	31	31
06 March	RV *Ed Ricketts*	5	27	10
14 May–13 June	RV *David Starr Jordan*	168	1262	55

Methods

Field collections

Larval and juvenile shortbelly rockfish were collected on four cruises between 1 February and 13 June 1989 (Table 1). All sampling was conducted along the central California coast from Cypress Pt. (Monterey Co.) to Pt. Reyes (Marin Co.). Larval samples were collected with oblique tows to maximum depths of 50–200 m, and were towed at depth for 30 seconds, at an approximate ship speed of one knot. Larval samples were collected with a 1 m plankton net (0.505 mm mesh) or, for the 18 February cruise, a 2×2 m Isaacs-Kidd trawl (2 mm mesh). For further information on larval hauls, see Appendix A. Larvae were sorted and placed in 80% ethanol. Juvenile samples were collected with a 26×26 m midwater trawl (0.945 cm mesh codend liner), towed horizontally at depth for 15 minutes at a speed of approximately one knot. Sampling for the juvenile survey was at fixed stations spread throughout the study area, with target depths of 10, 30, and 100 m, but with most samples taken at the standard depth of 30 m. Juvenile rockfish were removed from hauls and immediately frozen. For further details on procedures for the juvenile survey, see Wyllie Echeverria et al. (1990).

To determine when daily otolith increments begin to form, gestating larvae (rockfish are viviparous livebearers) were collected and their otoliths examined. Adult female rockfish were collected during the May–June survey and from commercial fishermen at Fort Bragg, California in May. Preextrusion larvae were removed and placed in 80% alcohol for later examination.

Laboratory procedures

The stage of development of the gestating larvae was determined by morphology and pigmentation (Moser et al. 1977). Larvae from four females (two from the May–June cruise and two collected from commercial fishermen in May) were found to be in an advanced stage of development and were used for further analysis.

The standard length (SL) of all larvae and juveniles was measured to the nearest 0.1 mm. Ages were determined for juveniles spanning the entire size range collected and for all planktonic larvae. Sagittae were removed from each fish and affixed whole to slides with a drop of clear fingernail polish. Intact otoliths from larvae ($<$20 mm) had discernable growth increments with no further preparation. For fish with SL $>$20 mm, otoliths were sanded in the sagittal plane with 400-grit sandpaper until the nucleus became visible. Concentrated HCl was used to etch the otoliths until growth increments were easily discernable.

All otoliths were viewed at 600–1250× magnification with a compound microscope equipped with a video camera and monitor. Only fish with a dark check mark that clearly encircled the primordium were used in our analysis of growth (see also Penney and Evans 1985). Fish with this mark and no additional increments were given a nominal age of zero. Increments were counted from this mark to the most distal point along the postrostral growth axis. We used a digitizer to record the exact position of each increment; otolith radius (OR) was measured to the nearest 0.1 μm.

Validation

To validate that the increments were formed daily, we only considered samples collected during the May–June survey, because it was the only multiple-day cruise. From the data we identified a well-defined, temporally discrete cohort, and estimated the average change in length of individuals over the duration of the cruise. We compared this rate with the rate of change in length with nominal age from otoliths.

We identified a temporally discrete cohort as follows. Using the 55 aged fish (mainly juveniles) from the May–June cruise, and assuming that the number of increments approximated age in days after extrusion, we linearly regressed age on SL. From the resulting regression equation, we estimated the ages of all juveniles caught (all specimens were measured, but only a subsample of 55 fish from this cruise was aged). By subtracting estimates of age from known dates of capture (measured from the beginning of the year), we estimated the dates when the dark check mark formed for all fish sampled. A plot of frequency of occurrence against estimated dates of check mark deposition was used to identify the cohort. We stress that this procedure was used only to identify the cohort for further consideration. The rate of change in length-per-unit-time for fish sampled from the cohort was found by calculating the rate at which the lengths of captured individuals changed over the course of the 30 day cruise.

Data analysis

Initial exploratory model development involved fitting a number of equations (by least squares) to the data to characterize two functional relationships: $OR = f(age)$ and $SL = g(OR)$. For the former, we used not only the radius of the otolith at the time of collection (terminal OR), but also back-calculated radii measured at earlier ages. Due to the serial correlation present in these data (multiple observations of OR-at-age from the same fish), we used the grouped jackknife technique (Miller 1974) to estimate standard errors of the parameters. In contrast, we used only terminal values of OR and SL when fitting the latter relationship. Once known, the composition of these two functions $\{f^{o}g\}$ defined explicitly the dependence of SL on age, i.e., $\widehat{SL} = g(f(age))$. This procedure provided a better description of the age-length relationship than did the more usual approach of fitting a growth model to back-calculated SL-at-age data, even when complex formulations were tried (e.g., the two-stage Gompertz function suggested by Zweifel and Lasker 1976).

A single-stage Gompertz growth equation (Ricker 1979) provided a good description of otolith growth. The model has three parameters (OR_0, k, and g) and can be expressed as:

$$OR = OR_0 \cdot \exp\{k \cdot [1 - \exp(-g \cdot age)]\}.$$

Our data showed increasing variance in OR with increasing age, so the data and the equation were logarithmically transformed prior to fitting (Zweifel and Lasker 1976).

To regress SL on OR, we developed a model consisting of four linear segments, each describing a different growth stanza (see Appendix B for details). Before selecting this segmented model, we first considered, and then discarded due to lack of fit, a number of continuous models, including the simple two-parameter linear model, the Gompertz function, and three-parameter power and exponential models with separate Y-intercept terms.

Once we had established a relationship between SL and OR, we used this relationship to back-calculate SL at ages younger than the terminal age-at-capture. We used the "body-size proportional" method described by Francis (1990) in our back-calculations, in which the length at age i (some age younger than c, the age of collection) for fish j (SL_{ij}) is given by:

$$SL_{ij} = g(OR_{ij}) \cdot (SL_{cj}/g(OR_{cj})),$$

where, as above, $g(\cdot)$ is the regression equation we developed to predict expected SL from OR, and SL_{cj} is the measured length of fish j at the time of capture. Note that this method corrects for the deviation between the length predicted by the regression model and actual length at the time of capture. The well-known Fraser-Lee method, which also takes into account actual length of an individual at the time of capture, is inappropriate here because of the non-linear relationship between SL and OR (Campana 1990, Francis 1990). The fit of $\widehat{SL} = g(f(age))$ to the "observed" back-calculated estimates of SL_{ij} was then evaluated by examining a plot of the residuals ($SL_{ij} - \widehat{SL}$).

Results

We measured SL of 1511 larval and juvenile shortbelly rockfish. Ages were determined for 249 fish that ranged in size from 4.5 to 74.5 mm SL. Of these, 194 (4.5–15.2 mm SL) were from the three single-day cruises and 55 (14.6–74.5 mm) were from the May–June cruise (Table 1).

None of the gestating preextrusion larvae that we examined possessed the dark check mark that we used as the starting point for increment counts. Because of this, and the presence of increments in most of the

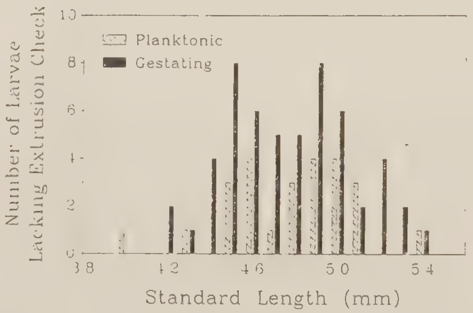

Figure 1
Size distributions of fully developed gestating (*n* 54) and planktonic (*n* 25) larvae of shortbelly rockfish lacking the extrusion check.

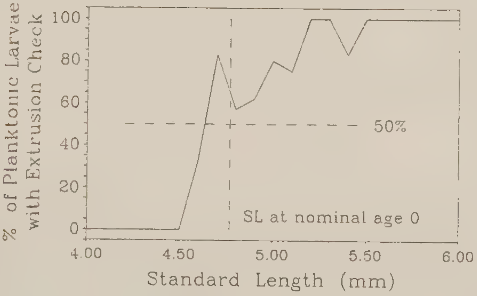

Figure 2
Change with length in the percentage of planktonic shortbelly rockfish larvae (*n* 25) exhibiting the extrusion check.

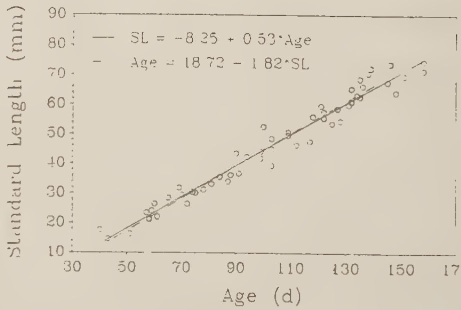

Figure 3
Least-squares regressions relating standard length and age for juvenile shortbelly rockfish collected during the May–June survey off central California, 1989.

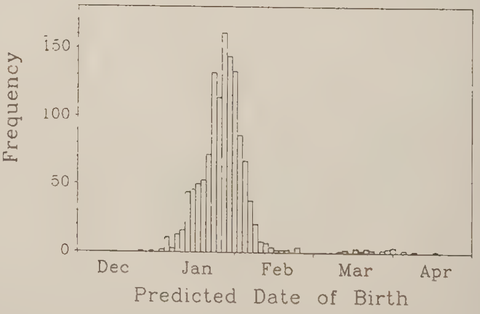

Figure 4
Frequency distribution of birthdates (date of extrusion check) for all shortbelly rockfish caught during the May-June survey off central California, 1989. Note the existence of a small but discrete second cohort spawned in March and April.

smallest planktonic larvae, we believe this mark was formed at, or shortly after, extrusion. The size distribution of the few planktonic larvae that lacked this feature (henceforth called the extrusion check) was similar to the size distribution of full-term, gestating larvae (Fig. 1). Thus, shortbelly rockfish do not appear to grow substantially from the time of extrusion to the time the extrusion check is formed. Likewise, all planktonic larvae greater than 5.5 mm in length had an extrusion check and more than 50% had the extrusion check, at a size of 4.7 mm (Fig. 2). The average size of the full-term gestating larvae we measured was 4.7 mm, and we take this as an estimate of the size-at-extrusion, which is independent of our growth models.

Validation

We compared how the mean SL of fish in a cohort changed over a 30-day period, with the growth rate estimated from a regression of SL on nominal age determined independently by examining otoliths. For the 55 fish we aged from the extended May–June cruise, a linear relationship existed between assumed daily age and SL, with a slope of 1.82 days/mm (SE 0.0484) and an r^2 of 0.963 (Fig. 3). The distribution of estimated birthdates for all juveniles caught during the cruise (*N* 1262) contained a small secondary mode (*N* 25) in March and April (Fig. 4). In our primary analysis, we considered only those fish with birthdates occurring in January or February (*N* 1237).

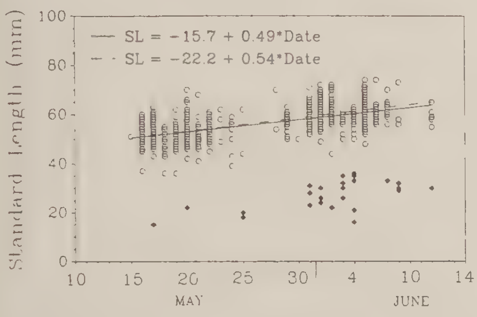

Figure 5

Regressions of standard length on calendar date of capture for all juvenile shortbelly rockfish taken during the May–June survey off central California, 1989 (solid line; r^2 0.265) and for the subset of juveniles that were extruded during the primary January–February spawn (open circles and dashed line; r^2 0.484). Diamonds represent the fish (n 25) spawned during March and April.

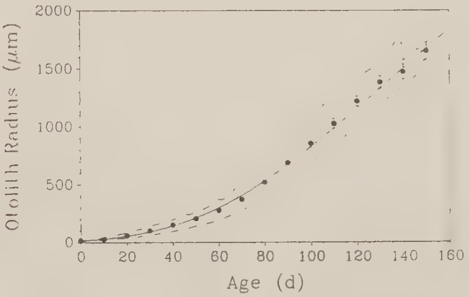

Figure 6

Predicted otolith radius as a function of age (solid line) from the Gompertz growth model (multiple observations from each specimen). Filled circles are means of the observed data at 10-day intervals, bracketed by ± 2 standard errors. Note that standard errors for younger ages do not appear due to the resolution of the figure. Dashed lines enclose the range of data.

For the juveniles from the first cohort, the slope of the regression of SL on date of capture was 0.54 mm/day (SE 0.0158; Fig. 5). This compares with a slope of 0.53 mm/increment (SE 0.0140) obtained from a regression of length against the number of increments counted for the 55 aged fish (Fig. 3). Moreover, the slope of a regression of the predicted ages of the fish from the first cohort on their date of capture was 0.96 increments/day (SE 0.028). This rate is not significantly different ($P>0.05$) from the expected 1:1 correspondence between increments and days (t −1.43, df 1235).

Most of the fish from the second cohort (Fig. 4) were captured late in the May–June cruise, probably because selectivity of the net did not allow their capture at the beginning of the cruise when they were smaller. Because fish from the second cohort were smaller and were caught later in the cruise, excluding them improved the agreement between the observed rate of change in length over time and the growth rate estimated from daily otolith increments of aged fish (Fig. 3). We feel that the exclusion was warranted because of the clear separation between the cohorts (Fig. 4). In any case, relatively few fish (25 out of 1262) were excluded, and the effect on our estimated rate of change in length of the cohort was slight (~10%; Fig. 5).

Growth of the otolith

Otoliths of shortbelly rockfish grow at a generally increasing rate from birth to ~90 days in age (Fig. 6). Thereafter, there is substantially less curvature in the data. Results of fitting the Gompertz growth function to the data yielded estimates of $OR_0 = 16.00\,\mu m$ (SE 0.0374), k = 5.4223 [dimensionless] (SE 0.0235), and g = 0.01298/day (SE 0.000106), with an r^2 of 0.991. The curve (solid line in figure) fit the data well except for a minor lack of fit at about 70 days of age.

Standard length vs. otolith radius and back-calculation of length

The segmented linear model (after Bacon and Watts 1971) provided a good fit when SL was regressed on OR (Fig. 7, Table 2). There was no discernable pattern to the residuals, and the r^2 value was quite high (0.998). In addition, the model's estimate of body length at the mean otolith radius at the extrusion check (17 μm) was 4.9 mm SL; this approximated independent estimates of length-at-extrusion (5.4 mm [Moser et al. 1977], 4.0 mm [MacGregor 1986], and 4.7 mm SL [this study, Figs. 1, 2]). The intersections of the four linear segments relating SL to OR were at 38.7, 73.1, and 431.3 μm OR, and the corresponding lengths were 7.7, 8.4, and 29.9 mm SL, respectively.

Larvae were collected with two types (sizes) of nets. A possible source of bias in our results could arise from different selectivities of the nets (Somerton and Kobayashi 1989). For example, differential sampling by the nets may be responsible for the segmenting seen in Figure 7, although we do not believe this is the case. Even though, on average, the nets collected different sized fish, both types of nets captured fish in the range

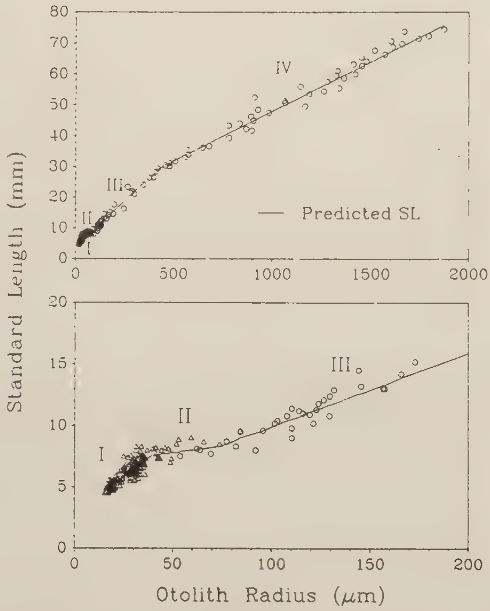

Figure 7

Plot of terminal standard length and otolith radius for all aged shortbelly rockfish (*N* 249). Shown is the predicted curve from the segmented model spanning the full range of data (upper panel), with Roman numerals for each of the four distinct growth stanzas. The lower panel enlarges the earliest growth stages (<200µm OR). Circles are fish taken in Isaacs-Kidd trawls, and triangles are from plankton nets.

Table 2

Parameter estimates for the segmented regression model describing the relationship between standard length (mm) and otolith radius (OR, µm); Y-intercept (a), slopes for each segment (b_1-b_4), and intersection points of the segments (c_1-c_3) on the X (OR) axis. Note that, except for c_1-c_3, these are algebraic transformations of the actual parameters fitted by the regression procedure (see Appendix B). Estimates of length for a given OR based on the values given below ignore the smoothing described in Appendix B, but will be close approximations of the values that would be obtained using the original parameterization.

Transformed parameter	Estimate
a	2.92
b_1	0.1233
b_2	0.0219
b_3	0.0599
b_4	0.0327
c_1	38.72
c_2	73.10
c_3	431.31

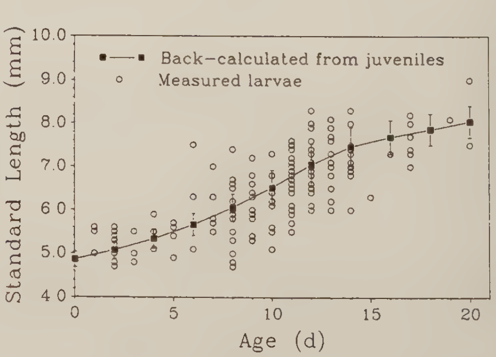

Figure 8

Scattergram of terminal standard length and age for larvae ≤20 days (open circles). Solid line depicts the back-calculated mean size-at-age (±1 SD) during the larval stage of juvenile fish (terminal age ≥60 days).

of 7.5–10.0mm SL (lower panel of Figure 7). Within this range, the relationship of SL to OR did not differ significantly between the nets (*t* 0.50, df 4, $P>0.05$).

Standard length vs. age

Our back-calculation of standard length-at-age (SL_{ij}) is based on the implicit assumption that the mean back-calculated length at any particular age is similar to the mean length of fish actually captured at those earlier ages. Violation of this assumption is the so-called Rosa Lee's phenomenon (Ricker 1979), which can arise when mortality rates are size-selective and from a number of other causes, such as biased sampling. However, our data show that mean length-at-age during the first 20 days of life, back-calculated from juveniles at least 60 days old, passes through the observed values of SL and age at the time of capture for young larvae (Fig. 8). This result suggests that Rosa Lee's phenomenon is unlikely to distort our findings to any appreciable degree.

The predicted fit of the composite function [$\widehat{SL} = g(f(age))$] to the back-calculated size data was good (Fig. 9). Note that individual fish followed their own growth trajectories, producing serial correlation in the residuals. The slight lack of fit around age = 70 days (see Figure 6) is also seen more easily in this figure.

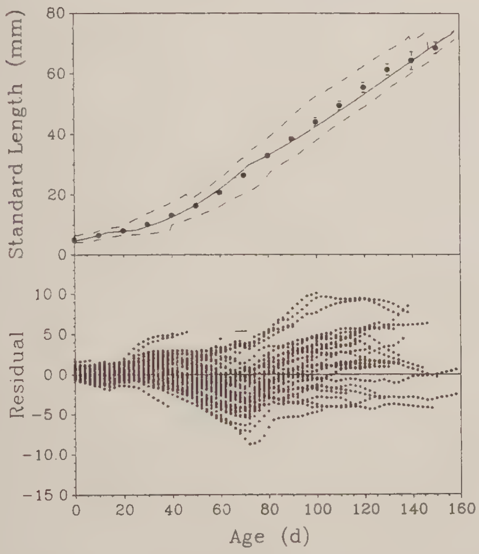

Figure 9

Relationship between back-calculated standard length and age for shortbelly rockfish. Solid line in the upper panel represents the composite function of relationships shown in Figures 6 and 7. Filled circles are means of the observed data at 10-day intervals, bracketed by ±2 standard errors. Dashed lines enclose the range of data. Residuals (observed–predicted) of the fit are shown below.

Discussion

Our goal was to develop a model that could be used to provide accurate estimates of back-calculated growth from the otolith microstructure of larval and juvenile shortbelly rockfish. A crucial assumption of the study was that the increments were formed daily. Many authors have stressed the importance of validating the daily periodicity of otolith growth increments (Jones 1986, Geffen 1987). Without validation, growth rates may be biased and their use in models of juvenile dynamics and recruitment could lead to serious errors. For validation purposes, we followed a cohort of fish through the May–June time period, measuring their progressive change in average length. We found that the rate of change in length of this cohort agreed with the estimated growth rate based on a regression of length against number of growth increments enumerated for aged fish. From this result, we conclude that the increments we counted were formed daily. It is noted, however, that the daily periodicity of these increments is validated only for the size ranges and dates observed during the extended May–June cruise, but we have no reason to assume that the increments are not daily at earlier stages of growth.

Other evidence exists that daily increments form in otoliths of *Sebastes* spp. Yoklavich and Boehlert (1987) demonstrated the daily periodicity of increment formation in otoliths of black rockfish *S. melanops* by marking the otoliths with oxytetracycline (OTC) and by autoradiography. Also, Laidig (unpubl. data) found no difference between increment counts and the number of days following a fluorescent OTC mark, verifying that the increments of brown rockfish *S. auriculatus* were interpreted correctly as daily.

Our segmented model of fish size versus otolith size, for use in back-calculating fish length, may describe significant events during the early life of *S. jordani*. The first major events following extrusion, in the early life of rockfish, are first feeding, flexion, and transformation from larva to juvenile. Moser et al. (1977) noted that shortbelly rockfish larvae undergo flexion at 8.0–10.0 mm SL. This range essentially corresponds to the size of fish in segment II. The slope of this segment was much reduced, suggesting that although fish length increases little during flexion, the otolith continues to grow. Likewise, Moser et al. (1977) found that juvenile transformation began after 27 mm SL, and we observed that the intersection of segments III and IV occurred at a length of about 30 mm SL. It is possible, of course, that the segments we have described are peculiar to the time and place that we collected the fish. For example, the slope of the fish size to otolith size relationship could have changed at specific points in time in response to altering oceanographic conditions (see also the discussion on "buffering" below). Before this type of alternative explanation can be discarded, similar SL–OR regressions need to be established in other years.

Relative to the entire organism, the sagittal otolith is a simple structure, especially during early life history. During the first 160 days of life, the sagitta develops from a spherical primordium into an oval-saucer shape. During this time a single Gompertz curve (Fig. 6) adequately described growth along one of its dimensions (i.e., the postrostral axis).

In contrast, the whole organism is morphologically and developmentally complex. Although a simple Gompertz curve, when fitted to back-calculated length (SL_{ij}) against age, resulted in a high r^2 value, an unacceptable pattern was evident in a plot of the residuals. Other authors also have found that smooth models (e.g., Gompertz and von Bertalanffy curves) did not accurately fit SL-at-age data in young-of-the-year fish (Uchiyama and Struhsaker 1981, Bailey 1982, Rosenberg and Laroche 1982, Campana 1984, Boehlert and Yoklavich 1985). Although these simplified models often perform well on adult fish, they are sometimes unable to depict the complex growth processes characterizing the complete life history. In such cases, segmented models should be considered because they allow for life history changes and growth stanzas (Ricker 1979). For example, Watanabe et al. (1988) found that for Pacific saury *Cololabis saira*, two Gompertz curves produced a better fit to the relationship of length and the number of daily otolith increments than did a single Gompertz curve. Zweifel and Lasker (1976) showed that a two-stage Gompertz curve described the growth of anchovy *Engraulis mordax* larvae better than a simple single-stage Gompertz curve. These authors also noted that although other models had high coefficients of determination, they exhibited unacceptable predictions for small larvae. Likewise, Nishimura and Yamada (1988) found that three linear segments described the relationship between otolith length and total length for walleye pollock *Theragra chalcogramma*, and that the intersection points between segments represented changes from larval to juvenile growth and juvenile to adult growth.

Changes in growth stages or stanzas are characterized by a fundamental alteration or discontinuity in development, such as hatching, first feeding, maturation, or a change in habitat (Ricker 1979). Above we presented and reviewed some evidence for this idea from studies of fish. The concept is likely to have validity for many organisms. For example, allometric relationships for physiological rates in *Daphnia* are stage-dependent (McCauley et al. 1990).

Some authors (Reznick et al. 1989, Secor and Dean 1989) have shown that otolith growth rate is relatively insensitive to factors that cause more extensive variation in somatic growth rate (e.g., alterations in temperature and food ration). Under extreme conditions, however, daily increment deposition arrests or is otherwise seriously perturbed (Tanaka et al. 1981, Campana 1983, Neilson and Geen 1985; reviews in Campana and Neilson 1985 and Jones 1986). Nonetheless, in many instances the otolith can be considered a conservative growth structure that is buffered from environmental factors affecting somatic growth. The otolith continues to record significant events, such as transitions to other life stages, even when somatic growth is seriously impaired. Conversely, this buffering tends to obscure the otolithic record of somatic growth fluctuations arising from exogenous factors, e.g., temperature fluctuation, changes in prey density, and turbidity.

Insulation of the otolith to ambient conditions can lead to a somatic:otolith size ratio that is positively related to growth rate. Recently, Campana (1990) showed that this can lead to biased estimates of length-at-age and the appearance of Rosa Lee's phenomenon, when lengths are back-calculated by the Fraser-Lee method. He noted that this problem is unlikely to be significant when the intercept is well fixed by aging young larval fish, or through use of independent biological measurements. In our study, many of the aged fish were young larvae. In addition, the estimated length of a fish with an otolith radius equal to the mean radius at the extrusion check was in good agreement with the mean length of late-stage gestating pre-extrusion larvae. Lastly, we found no evidence that back-calculated lengths of fish captured as juveniles differed from directly measured lengths of fish captured as larvae.

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Citations

Bacon, D.W., and D.G Watts
1971 Estimating the transition between two intersecting straight lines. Biometrika 55:525–534.

Bailey, K.M.
1982 The early life history of the Pacific hake, *Merluccius productus*. Fish. Bull., U.S. 80:589–598.

Bailey, K.M., and E.D. Houde
1989 Predation on eggs and larvae of marine fishes and the recruitment problem. Adv. Mar. Biol. 25:1–83.

Boehlert, G.W.
1981 The effects of photoperiod and temperature on laboratory growth of juvenile *Sebastes diploproa* and a comparison with growth in the field. Fish. Bull., U.S. 79:789–794.

Boehlert, G.W., and M.M. Yoklavich
1983 Effects of temperature, ration, and fish size on growth of juvenile black rockfish, *Sebastes melanops*. Environ. Biol. Fish. 8:17–28.

1985 Larval and juvenile growth of sablefish, *Anoplopoma fimbria*, as determined from otolith increments. Fish. Bull., U.S. 83:475–481.

Campana, S.E.
1983 Feeding periodicity and the production of daily growth increments in otoliths of steelhead trout (*Salmo gairdneri*) and starry flounder (*Platichthys stellatus*). Can. J. Zool. 61: 1591–1597.

1984 Microstructural growth patterns in the otoliths of larval and juvenile starry flounder, *Platichthys stellatus*. Can. J. Zool. 62:1507–1512.

1990 How reliable are growth backcalculations based on otoliths? Can. J. Fish. Aquat. Sci. 47:2219–2227.

Campana, S.E., and J.D. Neilson

1985 Microstructure of fish otoliths. Can. J. Fish. Aquat. Sci. 42:1014–1031.

Francis, R.I.C.C.

1990 Back-calculation of fish length: A critical review. J. Fish Biol. 36:883–902.

Geffen, A.J.

1987 Methods of validating daily increment deposition in otoliths of larval fish. *In* Summerfelt, R.C., and G.E. Hall (eds.), The age and growth of fish, p. 223-241. Iowa State Univ. Press, Ames.

Grover, J.J., and B.L. Olla

1986 Morphological evidence for starvation and prey size selection of sea-caught larval sablefish, *Anoplopoma fimbria*. Fish. Bull., U.S. 84:484–489.

Haldorson, L., and L.J. Richards

1987 Post-larval copper rockfish in the Strait of Georgia: Habitat use, feeding, and growth in the first year. *In* Proc., Int. Rockfish Symp., Anchorage, Oct. 1986, p. 129–141. Lowell Wakefield Fish. Symp. Ser 5, Alaska Sea Grant Rep. 87-2, Univ. Alaska, Fairbanks.

Hjort, J.

1914 Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-V. Reun. Comm. Int. Explor. Mer 20:1–228.

Hollowed, A.B., K.M. Bailey, and W.S. Wooster

1987 Patterns in recruitment of marine fishes in the northeast Pacific Ocean. Biol. Oceanogr. 5:99–131.

Houde, E.D.

1977 Food concentrations and stock density effects on survival and growth of laboratory-reared larvae of bay anchovy, *Anchoa mitchilli*, and lined sole, *Achirus lineatus*. Mar. Biol. (Berl.) 43:333–341.

1978 Critical food concentrations for larvae of three species of subtropical marine fishes. Bull. Mar. Sci. 28:395–411.

1987 Fish early life dynamics and recruitment variability. *In* Hoyt, R.D. (ed.), Proc., 10th annual larval fish conference, p. 17–29. Am. Fish. Soc. Symp. 2, Bethesda.

1989 Subtleties and episodes in the early life of fishes. J. Fish Biol. 35:29–38.

Hunter, J.R.

1981 Feeding ecology and predation of marine fish larvae. *In* Lasker, R. (ed.), Marine fish larvae, p. 33–79. Wash. Sea Grant Prog., Univ. Wash. Press, Seattle.

Hunter, J.R., and C.A. Kimbrell

1980 Egg cannibalism in the northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 78:811–816.

Jones, C.

1986 Determining age of larval fish with otolith increment technique. Fish. Bull., U.S. 84:91–103.

Lasker, R.

1975 Field criteria for survival of anchovy larvae: The relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull., U.S. 73:453–462.

1978 The relation between oceanographic conditions and larval anchovy food in the California Current: Identification of factors contributing to recruitment failure. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 173:375–388.

McCauley, E., W.W. Murdoch, R.M. Nisbet, and W.S.C. Gurney

1990 The physiological ecology of Daphnia: Development of a model of growth and reproduction. Ecology 71:703–715.

MacGregor, J.S.

1986 Relative abundance of four species of *Sebastes* off California and Baja California. Calif. Coop. Oceanic Fish. Invest. Rep. 27:121–135.

Miller, R.G.

1974 The jackknife—A review. Biometrika 61:1–15.

Miller, T.J., L.B. Crowder, J.A. Rice, and E.A. Marschall

1988 Larval size and recruitment mechanisms in fishes: Toward a conceptual framework. Can. J. Fish. Aquat. Sci. 45:1657–1670.

Moser, H.G., E.H. Ahlstrom, and E.M. Sandknop

1977 Guide to the identification of scorpionfish larvae (family Scorpaenidae) in the eastern Pacific with comparative notes on species of *Sebastes* and *Heliocolenus* from other oceans. NOAA Tech. Rep. NMFS Circ. 402, 71 p.

Neilson, J.D., and G.H. Geen

1985 Effects of feeding regimes and diel temperature cycles on otolith increment formation in juvenile chinook salmon, *Onchorhychus tshawytscha*. Fish. Bull., U.S. 83:91–101.

Nishimura, A., and J. Yamada

1988 Geographical differences in early growth of walleye pollock, *Theragra chalcogramma*, estimated by back-calculation of otolith daily growth increments. Mar. Biol. (Berl.) 97: 459–465.

Pannella, G.

1971 Fish otoliths: Daily growth layers and periodical patterns. Science (Wash. DC) 173:1124–1127.

Penney, R.W., and G.T. Evans

1985 Growth histories of larval redfish (*Sebastes* spp.) on an offshore Atlantic fishing bank determined by otolith increment analysis. Can. J. Fish. Aquat. Sci. 42:1452–1464.

PFMC (Pacific Fishery Management Council)

1989 Status of the Pacific coast groundfish fishery through 1989 and recommended acceptable biological catches for 1990. Pac. Fish. Manage. Counc., Portland, 299 p.

Phillips, J.B.

1964 Life history studies on ten species of rockfish (genus *Sebastodes*). Calif. Dep. Fish Game, Fish Bull. 126, 70 p.

Reznick, D., E. Lindbeck, and H. Bryga

1989 Slower growth results in larger otoliths: An experimental test with guppies (*Poecilia reticulata*). Can. J. Fish. Aquat. Sci. 46:108–112.

Ricker, W.E.

1979 Growth rates and models. *In* Hoar, W.S., D.J. Randall, and J.R. Brett (eds.), Fish physiology, p. 677–742. Academic Press, NY.

Rosenberg, A.A., and J.L. Laroche

1982 Growth during metamorphosis of English sole, *Paraphrys vetulus*. Fish. Bull., U.S. 80:150–153.

Rothschild, B.J.

1986 Dynamics of marine fish populations. Harvard Univ. Press, Cambridge, MA, 277 p.

Secor, D.H., and J.M. Dean

1989 Somatic growth effects on the otolith-fish size relationship in young pond-reared striped bass, *Morone saxatilis*. Can. J. Fish. Aquat. Sci. 46:113–121.

Sinclair, M.

1988 Marine populations. Univ. Wash. Press, Seattle, 252 p.

Sissenwine, M.P.

1984 Why do fish populations vary? *In* May, R.M. (ed), Exploitation of marine communities, Report of the Dahlem workshop on exploitation of marine communities, Berlin, April 1–6, 1984, p. 59–94. Springer-Verlag, Berlin.

Somerton, D.A., and D.R. Kobayashi
1989 A method for correcting catches of fish larvae for the size selection of plankton nets. Fish. Bull., U.S. 87:447-455.

Tanaka, K., Y. Mugiya, and J. Yamada
1981 Effects of photoperiod and feeding on daily growth patterns in otoliths of juvenile *Tilapia nilotica*. Fish. Bull., U.S. 79:459-466.

Theilacker, G.H.
1978 Effect of starvation on the histological and morphological characteristics of jack mackerel, *Trachurus symmetricus*, larvae. Fish. Bull., U.S. 76:403-414.
1981 Effects of feeding history and egg size on the morphology of jack mackerel, *Trachurus symmetricus*, larvae. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 178:432-440.

Thorrold, S.R., and D.McB. Williams
1989 Analysis of otolith microstructure to determine growth histories in larval cohorts of a tropical herring (*Herklotsichthys castelnaui*). Can. J. Fish. Aquat. Sci. 46:1615-1624.

Uchiyama, J.H., and P. Struhsaker
1981 Age and growth of skipjack tuna, *Katsuwonus pelamis*, and yellowfin tuna, *Thunnus albacares*, as indicated by daily growth increments of sagittae. Fish. Bull., U.S. 79:151-162.

Underwood, A.J., and P.G. Fairweather
1989 Supply-side ecology and benthic marine assemblages. Trends Ecol. & Evol. 4:16-19.

Watanabe, Y., J.L. Butler, and T. Mori
1988 Growth of Pacific saury, *Cololabis saira*, in the northeastern and northwestern Pacific Ocean. Fish. Bull., U.S. 86:489-498.

Woodbury, D., and S. Ralston
1991 Interannual variation in growth rates and back-calculated birthdate distributions of pelagic juvenile rockfishes (*Sebastes* spp.) off the central California coast. Fish. Bull., U.S. 89: 523-533.

Wyllie Echeverria, T., W.H. Lenarz, and C. Reilly
1990 Survey of the abundance and distribution of pelagic young-of-the-year rockfishes, *Sebastes*, off central California. Tech. Memo. NOAA-TM-NMFS-SWFC 147, Southwest Fish. Sci. Cent., NMFS, NOAA, La Jolla, CA, 125 p.

Yoklavich, M.M., and G.W. Boehlert
1987 Daily growth increments in otoliths of juvenile black rockfish, *Sebastes melanops*: An evaluation of autoradiography as a method of validation. Fish. Bull., U.S. 85:826-832.

Zweifel, J.R., and R. Lasker
1976 Prehatch and posthatch growth of fishes—a general model. Fish. Bull., U.S. 74:609-621.

Appendix A

Detailed information on individual larval hauls.

Date	Research vessel	Gear type	Max. depth	Lat.	Long.	No. caught	No. aged
2/1	RV *Ed Ricketts*	Plankton net	150	36°48.2′	121°51.9′	22	15
2/1	″	″	150	36°48.1′	121°52.7′	42	27
2/1	″	″	100	36°47.8′	121°54.0′	27	5
2/1	″	″	100	36°47.8′	121°54.7′	48	34
2/1	″	″	200	36°47.9′	121°53.7′	32	18
2/1	″	″	80	36°48.4′	121°53.2′	36	33
2/1	″	″	100	36°48.3′	121°52.4′	13	4
2/18	RV *David Starr Jordan*	Isaacs-Kidd trawl	200	37°16.6′	122°49.1′	0	0
2/18	″	″	200	37°16.7′	122°49.0′	32	31
3/6	RV *Ed Ricketts*	Plankton net	100	36°48.2′	121°52.7′	2	1
3/6	″	″	120	36°47.8′	121°53.7′	5	4
3/6	″	″	140	36°47.2′	121°55.2′	6	6
3/6	″	″	130	36°46.4′	121°59.6′	4	4
3/6	″	″	60	36°47.2′	121°50.6′	12	8

Appendix B

Here we describe the regression model used to relate standard length to otolith radius, which consisted of a series of four linear segments, each describing a different growth stanza. We start with the following equation:

$$SL = \begin{cases} a + b_1x \text{ for } x<c_1 \\ a + b_1c_1 + b_2(x-c_1) \text{ for } c_1 \leq x<c_2 \\ a + b_1c_1 + b_2(c_2-c_1) + b_3(x-c_2) \text{ for } c_2 \leq x<c_3 \\ a + b_1c_1 + b_2(c_2-c_1) + b_3(c_3-c_2) + b_4(x-c_3) \text{ for } c_3 \leq x \end{cases} \tag{1}$$

where a is the y-intercept of the first segment, x is the otolith radius, b_1, b_2, b_3, and b_4 are the slopes of the four segments, and c_1, c_2, and c_3 are the points on the x axis corresponding to the intersections. Because not all individuals would be expected to make the transition from one stanza to the next at identical sizes, it is reasonable to smooth the relationship at the segment intersections. We therefore applied the technique described by Bacon and Watts (1971) to smooth the transition between linear segments, assuming that most fish made the transition from one stanza to the next over a small size range. Specifically, we assumed that the probability that an individual fish made the transition from one stanza to the next was described by the logistic cumulative distribution function, $F(z) = 1/(1+\exp(-z))$, where $z = (x-c_i)/g$. Note that g is a constant chosen so that 95% of all transitions occur within $\pm 0.3 \mu m$ OR of each intersection. (We assumed this rapid rate of transition rather than evaluating the transition rate from the data because preliminary analyses, with g as an estimated parameter, indicated that the density of measurements on the x axis was not sufficient to yield unique solutions. Runs with different starting parameters did not converge to the same parameter estimates.) Following Bacon and Watts (1971), we rewrote the model as:

$$SL = e + d_1(x-c_1) + d_2(x-c_1)s_1 + d_3(x-c_2)s_2 + d_4(x-c_3)s_3 \tag{2}$$

where the terms relate to equation 1 as follows:

$$\begin{aligned} s_i &= 2*(F((x-c_i)/g) - 1;\ i=1,2,3;\ g=0.1, \\ d_1 &= (b_1+b_4)/2,\ d_2=(b_2-b_1)/2, \\ d_3 &= (b_3-b_2)/2, \\ d_4 &= (b_4-b_3)/2, \text{ and} \\ e &= a + ((b_1+b_4)/2)c_1 - ((b_2-b_1)/2)c_1 - ((b_3-b_2)/2)c_2 - ((b_4-b_3)/2)c_3. \end{aligned}$$

Our estimates of the above parameters and their standard errors are in Appendix Table 1.

Appendix table 1

Parameter estimates for segmented SL vs. OR regression model, and their associated standard errors (SE).

Parameter	Estimate	SE
e	12.375	0.411
d_1	0.0780	0.0078
d_2	−0.0507	0.016
d_3	0.0190	0.014
d_4	−0.0136	0.00091
c_1	3.872	0.480
c_2	7.310	2.044
c_3	43.131	2.128

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Sexual dimorphism in *Sebastes*

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Synopsis

Sexual dimorphism and factors that may cause it were investigated in 34 species of the genus *Sebastes*. Sexual dimorphism in standard length and morphometric characters are fairly common in rockfish. In many species males are shorter than females. However in males head length, width of orbit, interorbital width, length of upper jaw, longest pectoral fin ray and longest dorsal spine tend to be larger at a specified size than in females. Water-column species tend to be more dimorphic than demersal species. We suggest that the observed differences in dimorphism in standard length may be related to differences in mating and territorial behavior. Dimorphisms in morphometric measurements may be related to compensation in feeding ability for reduced standard length of males, mating and territorial behavior.

Introduction

Sexual dimorphism is a topic of lasting interest to biologists (e.g. Darwin 1871, Lewin 1988). Many vertebrate taxa exhibit sexual dimorphism, and explanations for its cause abound and are sometimes contradictory: e.g. 'Furthermore, biological complexity is such that one can find evidence and devise arguments for proposing that large size leads to decreased survivorship. . . or to increased survivorship. . .' (Murray 1984).

Sexual dimorphism has been demonstrated in species of *Sebastes*. Male *S. umbrosus* have a longer anal fin base, anal fin rays, snout and deeper pre-pelvic body; females have greater pre-anal length (Chen 1971). The urinary bladder of male *S. mystinus* is larger than in females (Helvey 1982). Moser (1967) found sexual differences in the urogenital papilla of *S. paucispinis* and Chen (1986) noted that the dimorphism is a general feature of *Sebastes*. Wyllie Echeverria (1986) studied *S. flavidus, S. melanops, S. mystinus* and *S. serranoides*. Orbit width in all four species was larger in males, and the longest pectoral fin ray was larger in males for all but *S. mystinus*. Chen (1986) found no evidence for sexual dimorphism in meristic counts for *S. semicinctus*.

Adult size of female rockfish is often larger than males (Miller & Geibel 1973, Six & Horton 1977, Boehlert 1980, Fraidenberg 1980, Lenarz 1980, Wilkens 1980, Love & Westphal 1981, Wilkens & Weinberg 1986, Wyllie Echeverria 1986, Lenarz 1987, Nelson & Quinn 1987, Love et al. 1989). However, exceptions exist (see Chen 1971, O'Connell & Funk 1987).

We examine morphometric measurements of 34 species of *Sebastes*, occurring off central and northern California, for evidence of sexual dimorphism. From these data, we have concluded that there are trends in extent of sexual dimorphism among *Se-*

bastes species groups and have used these trends to develop hypotheses on factors effecting dimorphism.

Methods

Specimens were collected by trawl and hook and line off the coasts of California and Oregon. When possible fish were measured while fresh. Otherwise fish were frozen and then thawed before measuring. It is assumed that the effects of method of capture and storage are independent of sex. Standard length (SL) and 23 other measurements were taken (Table 1). Vernier calipers (± 0.01 mm) were used for all measurements except standard, fork and total lengths. Measuring boards (± 1 mm) were used for the latter measurements.

Linear regressions with SL as the independent variable and the other morphometric measurements as dependent variables were done for the sexes separately and combined. Approximately 1% of the observations were deleted as likely errors in measuring or recording. Analyses of covariance were done to test the hypotheses that the relationships between the 23 morphometric variables and SL are independent of sex at the 95% level of confidence. These analyses tested the null hypothesis that one regression explains the relationship between dependent and independent variables against the alternative hypothesis that a separate regression (intercept and slope) for each sex better explains the relationship. Kleinbaum & Kupper (1978) refer to the null hypothesis as 'the two regression lines are coincident'. Examination of the data indicated that the usual assumptions of linearity, normality and independence of residuals were satisfied. Because so many statistical tests were performed ($N = 782$), statistically significant results due to chance alone are to be expected (Type I errors). Assuming a binomial distribution for the test results and no effect of sex, the expected number of Type I errors is 39.1 (782×0.05) with a variance of 37.1 ($782 \times 0.05 \times 0.95$). Using a normal approximation, the expectation is 51 or fewer Type I errors at the 95% confidence level.

We attempted to eliminate Type I errors by using a sign test (Dixon & Massey 1957) for each morphometric variable. Each observation for the sign test was the result of the analysis of covariance from each species. A result was considered positive if female measurements were significantly larger than for males, and negative for the converse. The test was made at the 95% confidence level. Since significantly different regressions often intersected, it was necessary to compare expected morphometric measurements at a specified SL. The comparison was made at the average of the maximum and minimum SL in our samples for both sexes combined. Only measurements that produced significant sign tests were used for examination of trends among species groups. These measurements are referred to as sexually dimorphic characters in the remainder of the paper. This procedure is conservative and may result in our ignoring morpho-

Table 1. Morphometric measurements, measurement codes and source for description of measurement.

Measurement[1]	Measurement code
Standard length (P)	SL
Fork length (P)	FL
Total length (P)	TL
Head length (P)	HL
Body depth at ventral fin (H)	VD
Body depth at anal fin (H)	AD
Width of base of anal fin (P)	AW
Snout length (P)	NL
Width of orbit (P)	OW
Interorbital width (P)	IW
Length of upper jaw (P)	JL
Width of pectoral fin base (P)	PW
Longest pectoral fin ray length (P)	PL
Longest pelvic fin ray length (P)	PR
Length of pelvic spine (P)	PS
Length of first anal spine (H)	AF
Length of second anal spine (H)	AS
Length of third anal spine (H)	AT
Longest anal ray fin length (H)	AL
Longest dorsal spine (H)	DS
Longest dorsal fin ray (H)	DR
Width of caudal peduncle (P)	CW
Distance between anus and anal fin (H)	AA
Longest gill raker on first arch (H)	GL

[1] (P) = From Phillips (1957).
(H) = From Holt (1959).

metric measurements that actually are larger in one sex or the other. Rank sum tests (Dixon & Massey 1957) were made at the 95% confidence level to test for differences in proportions of significant sexually dimorphic characters among species groups.

The ratio of male to female SL was used as an index of sexual size dimorphism. We used the average SL of mature fish measured in this study to calculate the ratio. Rank sum tests were made at the 95% confidence level to test differences in sexual dimorphism in size among groupings of species.

Results

Sample sizes for the morphometric measurements ranged from 11 to 192 and averaged 83. Sample size by sex and detailed results of the regressions and analyses of covariance are available from the au-

Table 2. Results of analyses of covariance testing hypotheses that relationships between morphometric measurements and standard length are independent of sex. M indicates that the measurement is significantly greater for males; F indicates that the measurement is significantly greater for females. Measurement codes are defined in Table 1.

Species	Measurement code																						
	FL	TL	HL	VD	AD	AW	NL	OW	IW	JL	PW	PL	PR	PS	AF	AS	AT	AL	DS	DR	CW	AA	GL
S. alutus										M												M	
S. auriculatus									F	M												M	
S. aurora	F			F																			
S. babcocki				F		M		M		M													
S. carnatus	M	M					M		M			M											
S. caurinus									M	M													
S. chlorostictus					F																		
S. chrysomelas	F																M		M				
S. constellatus						F		M						M									
S. crameri										M		M				M	M	M	M		M	F	
S. diploproa				F				M				M											M
S. elongatus			M	F			M	M		M											F		
S. entomelas								M														M	
S. flavidus								M	M	M		M		M		M	M			M			
S. goodei					M			M			M	M	F							F		F	
S. hopkinsi														F									
S. jordani	M	M	M	M	M	M	M	M	M	M	M	F	M	F	M			M		M			M
S. levis	F	F												M						F			
S. maliger										M		M											
S. melanops			M					M	M	F		M			M			F					
S. melanostomus						M						M										F	
S. miniatus										M													
S. mystinus				F	F			M		M	F							F	M	F			
S. nebulosus						M							M										
S. ovalis					F			M					F	F							F		
S. paucispinis			M			M		M	M	M	M	M		M	M	F	M	M	M	M			
S. pinniger		M	M				M	M	M	M	M	M								F			
S. rosaceus																				M			
S. rosenblatti																							
S. ruberrimus									M	M									M				
S. rufus																						F	
S. saxicola			M		F	F	M	M		M								F			M		
S. semicinctus		F	M								M							F		F	M		
S. serranoides	F	M		M	M			M	M	M		M		M					M	M		M	M

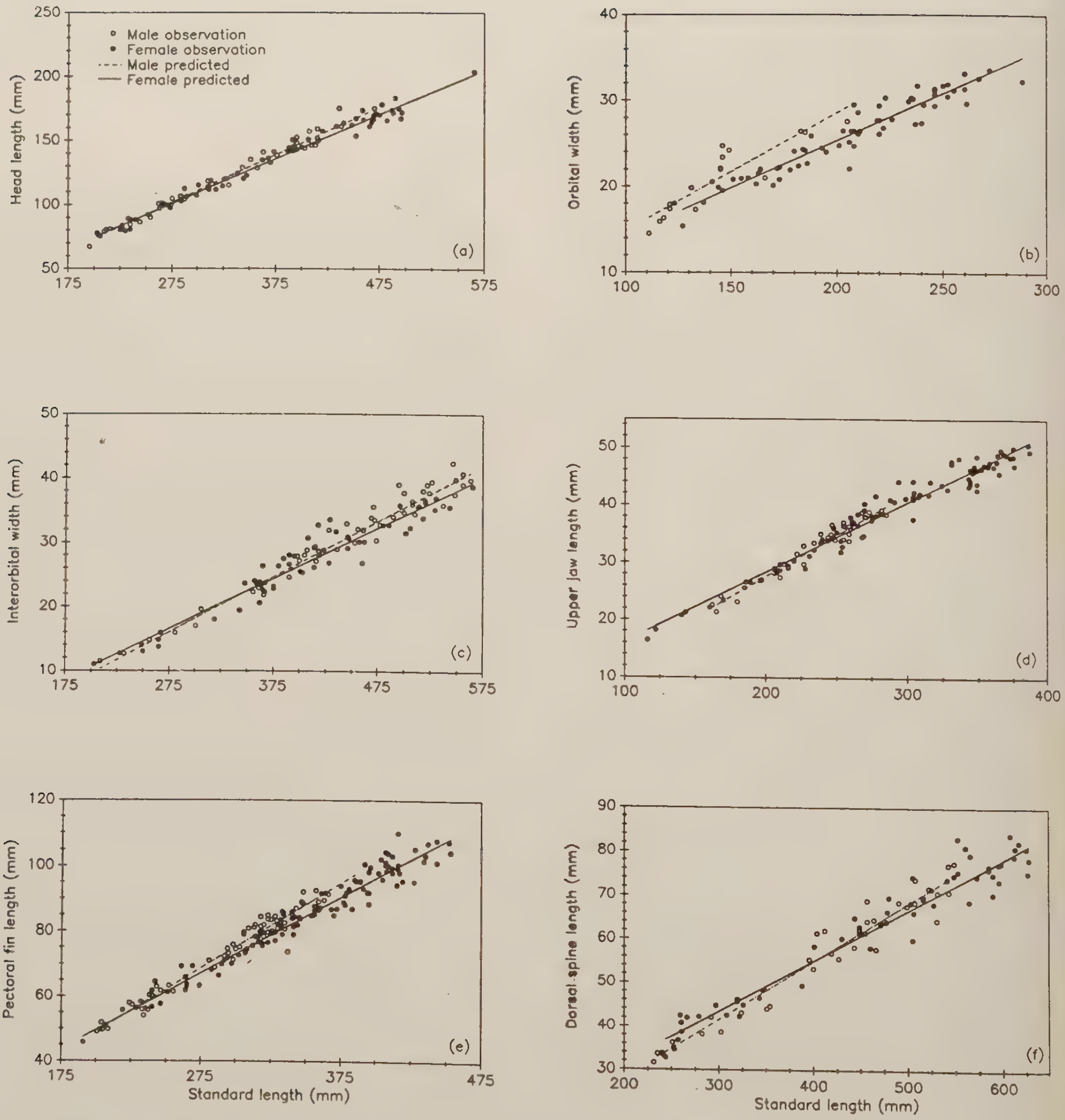

Fig. 1. Examples of relationships between sexually dimorphic characters and standard length for *Sebastes*: (a) head length for *S. pinniger*, (b) orbital width for *S. saxicola*, (c) interorbital width for *S. ruberrimus*, (d) upper jaw length for *S. mystinus*, (e) pectoral fin length for *S. flavidus* and (f) dorsal spine length for *S. paucispinis*.

thors. The analyses of covariances resulted in 166 rejections of the hypothesis that the relationship between a morphometric variable and SL is independent of sex (Table 2). This is more than three times the maximum number expected due to Type I errors. Male measurements were usually larger than female (124 vs. 42, respectively). Sign tests indicated that males often (64 cases) have greater head length, width of orbit, interorbital width, length of upper jaw, longest pectoral fin ray and longest dorsal spine. These six measurements are called sexually dimorphic characters and are considered in greater detail.

An example of the results is shown for each sexually dimorphic character in Figure 1. The species were randomly selected without replacement for the examples. The dimorphisms are quite noticeable in some cases, but subtle in others. The male slope is greater than the female in all of the examples. In most examples there is considerable overlap of the dimorphic measurement between sexes for small fish.

Males are smaller than females in 27 of the 34 species (Table 3). The ratio of male to female SL tends to decrease as the number of significant sex-

Table 3. Summary of number of sexually dimorphic characters significantly larger for males than females, ratio of male to female standard length (SL) and classification. Subgenera are as summarized by Seeb (1986).

Species	Number of significant characters	SL ratio	Classification		
			behavior[1]	depth[2]	subgenus[3]
S. aurora	0	0.98	D	D	S1
S. chlorostictus	0	1.02	D	S	S2
S. hopkinsi	0	0.70	D	S	N
S. levis	0	0.98	D	D	N
S. nebulosus	0	1.05	D	S	P
S. rosaceus	0	1.00	D	S	S2
S. rosenblatti	0	0.98	D	D	S2
S. rufus	0	0.87	W	D	N
S. alutus	1	1.06	W	D	S1
S. chrysomelas	1	1.07	D	S	P
S. constellatus	1	1.10	D	S	S2
S. entomelas	1	0.91	W	D	N
S. melanostomus	1	0.94	W	D	N
S. miniatus	1	0.94	D	S	N
S. ovalis	1	0.80	W	D	N
S. semicinctus	1	0.84	W	D	A
S. auriculatus	2	0.94	D	S	N
S. babcocki	2	0.95	D	D	N
S. carnatus	2	1.02	D	S	P
S. caurinus	2	0.98	D	S	P
S. diploproa	2	0.93	W	D	A
S. goodei	2	0.81	W	D	N
S. maliger	2	0.99	D	S	P
S. crameri	3	0.92	W	D	N
S. elongatus	3	0.87	D	D	N
S. mystinus	3	0.86	W	S	N
S. ruberrimus	3	0.98	D	S	S1
S. saxicola	3	0.69	W	D	A
S. flavidus	4	0.93	W	S	S3
S. jordani	4	0.87	W	D	N
S. melanops	4	0.91	W	S	S3
S. pinniger	5	0.94	W	S	N
S. serranoides	5	0.93	W	S	S3
S. paucispinis	6	0.92	W	D	N

[1] W = water-column and D = demersal.

[2] S = shallow and D = deep.

[3] A = *Allosebastes*, N = not classified, P = *Pteropodus*, S1 = *Sebastes*, S2 = *Sebastomus* and S3 = *Sebastosomus*.

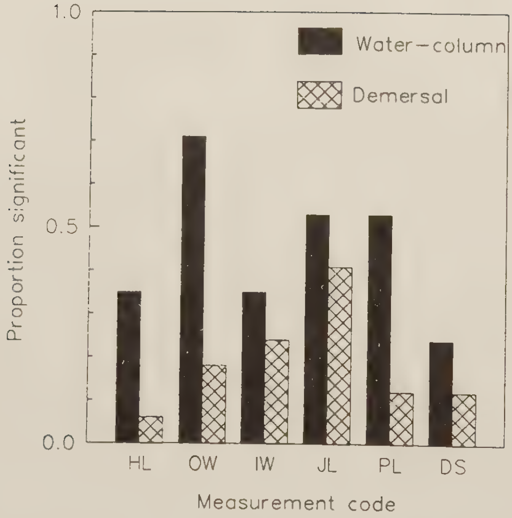

Fig. 2. Proportion of significant differences in sexually dimorphic characters of water-column and demersal species of *Sebastes*. Measurement codes are defined in Table 1.

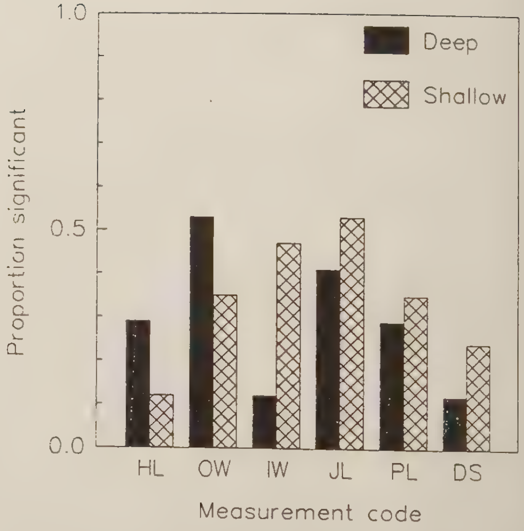

Fig. 3. Proportion of significant differences in sexually dimorphic characters of deep and shallow species of *Sebastes*. Measurement codes are defined in Table 1.

ually dimorphic characters increases, but a rank sum test was not significant.

Species were classified into two ecological dichotomies: water column or demersal and deep or shallow (Table 3). The two classifications are not independent. Most water-column species are deep, and most demersal species are shallow. A species is considered demersal if it seldom leaves the proximity of the bottom. A species is considered a deep species if adults are relatively common deeper than 125 m. These classifications are based on our knowledge of the species, and some judgment is involved. Love et al. (1991) independently classified 26 of the species of our study into ecological categories and divided the species into finer categories than we did. If their categories are combined into ours, the two studies similarly categorize species.

The average SL ratio of male to female is 0.89 for water-column species and 0.97 for demersal. The

Table 4 Average ratios of male to female standard length (SL) and number of significant sexually dimorphic characters per species for rockfish classified into water-column-deep, water-column-shallow, demersal-deep and demersal-shallow categories.

	Deep	Shallow	All species
Water-column			
Number	12	5	17
SL ratio	0.88	0.91	0.89
Number of dimorphic characters	2.08	4.20	2.71
Demersal			
Number	5	12	17
SL ratio	0.95	0.98	0.97
Number of dimorphic characters	1.00	1.17	1.12
Total			
Number	17	17	34
SL ratio	0.90	0.96	0.91
Number of dimorphic characters	1.76	2.06	1.91

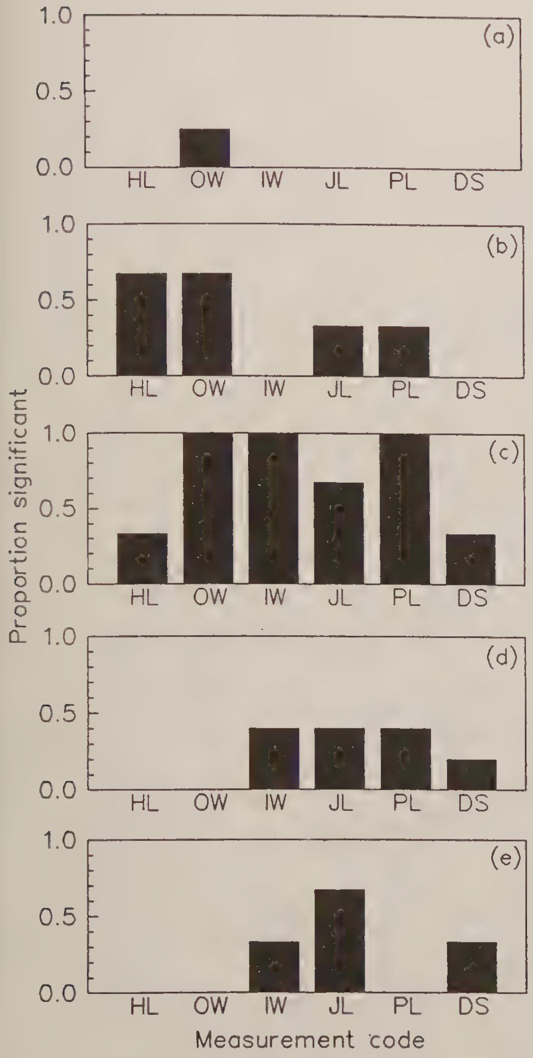

Fig. 4. Proportion of significant differences in sexually dimorphic characters of subgenera of *Sebastes*: (a) *Sebastomus* (b) *Allosebastes*, (c) *Sebastosomus*, (d) *Pteropodus* and (e) *Sebastes*. Measurement codes are defined in Table 1.

difference is significant. The proportion of significant differences in each of the sexually dimorphic characters is consistently greater among the water-column than in the demersal species (Fig. 2). The difference between the two groupings is significant. The differences in proportion are greatest for orbital width and pectoral fin length. The average ratio of male to female sizes is 0.90 for deep species and 0.96 for shallow species. The difference is significant. Shallow species are more often dimorphic for interorbital width than deep species (Fig. 3). However, the proportion of significant differences for the six characters is not significantly different between shallow and deep species.

The variation in the proportion of significant sexually dimorphic characters is significant between demersal and water-column species, but not so between shallow and deep species. While the difference in average size ratio is significant between shallow and deep species, within the water-column and demersal groupings the differences between deep and shallow species are minor (Table 4) and not significant. Thus sexual dimorphism does not appear to be related to the water depth classification.

Species were grouped into classical subgenera as summarized by Seeb (1986) from the literature for some of the species of our study (Table 3). Her biochemical analysis supported the *Sebastomus, Sebastosomus* and *Pteropodus* subgenera, but did not support *Allosebastes* and *Sebastes* well. We found the lowest average SL ratio of male to female size for *Allosebastes* (0.82) and the highest ratio for *Sebastes* (1.07). The ratio was 0.92 for *Sebastosomus* and 1.02 for *Sebastomus* and *Pteropodus. Sebastomus* had almost no significant sexually dimorphic characters, and *Sebastosomus* had many (Fig. 4).

All but one species (*S. alutus*) in *Sebastomus, Pteropodus* and *Sebastes* are demersal, and these three subgenera are not very dimorphic (Table 3 and Fig. 4). All species in *Allosebastes* and *Sebastosomus* are in the water-column group. The two subgenera are relatively dimorphic compared to the other three. *Allosebastes* is more dimorphic in size than *Sebastosomus*, and the converse is true for the proportion of sexually dimorphic characters (Fig. 4). The number of species in each subgenus is too small to test for differences in dimorphism.

Discussion

Wyllie Echeverria (1986) found sexual dimorphisms in the four species that she studied: *S. flavi-*

dus, *S. melanops*, *S. mystinus* and *S. serranoides*. The four species are water-column species, and all but *S. mystinus* are in the subgenus *Sebastosomus*. Females of these species reached a larger size than males. Wyllie Echeverria (1986) attributed the dimorphism in size to the fact that larger females produce more eggs. The data available at the time of her study indicated that males mature younger than females. Ostensibly, the younger age of maturity would provide males with more mating opportunities. She argued that increased sperm production resulting from increased size is not as important as increased opportunities to mate.

Many authors have advanced similar arguments for other groups of animals, but there are questions on the validity of the arguments. Shine (1988) showed that in some groups females are larger than males even though fecundity or egg volume is unrelated to size.

Our study, using data on more species than available to Wyllie Echeverria (1986), shows that many species of *Sebastes* are not dimorphic in size. Moreover, males do not always mature at an earlier age than females. Males of only 10 of 31 species studied by both Wyllie Echeverria (1987) and us matured earlier than females. In most species both sexes matured at the same age. Thus the size advantage for egg production is not the only factor related to sexual size dimorphism observed in some species of *Sebastes*. Of the species that exhibited early male maturity, the average ratio of male to female size is 0.94. The average ratio is 0.93 for the other species. The increased spawning opportunity hypothesis for early maturing males does not seem to hold for all species.

There is a considerable difference in the average ratio of male to female size for water-column (0.89) and demersal (0.97) species of rockfish. Demersal species, apparently both sexes for some species, have been observed to defend territories (Hallacher 1977, Haaker 1978, Larson 1980, Shinomiya & Ezaki 1990). Shinomiya & Ezaki (1991) observed male *S. inermis* defending territories during the mating season and that larger males had larger territories. Females did not appear to defend territories.

Aggressive behavior is rarer for water-column species, and agonistic interactions of any kind seem to occur mainly during the mating season (E. Hobson personal communication). Helvey (1982) observed courtship behavior of *S. mystinus*, a water-column species, during which males were active and females inactive. Helvey (1982) observed what appeared to be aggressive encounters between males when they were associated with a female, but he observed no physical contact between males. The courtship behavior of *S. mystinus* as described by Helvey (1982) was not as elaborate as that of *S. inermis*, a demersal species, as described by Shinomiya & Ezaki (1991).

While observations on territorial and mating behavior of *Sebastes* are limited to a few species, variations have been found. These variations may be related to the differences observed in sexual dimorphism. Territorial behavior has now been observed for several demersal species. In one species males are more territorial than females; in other species sexual differences in territoriality have not been observed. Since larger males have been observed to hold larger territories, the tendency for the ratio of male to female SL to be high for demersal species may be related to an increased tendency for territorial behavior by demersal males. The tendency for the ratio of male to female SL to be low for water-column species may be related to the reduced tendency for territorial behavior by water-column males and a cost due to large size. Recent work on *S. jordani* indicates that old specimens are smaller than middle aged specimens of this unexploited species (D. Pearson personal communication). This result suggests that survival is relatively low for faster growing individuals.

In summary variations of dimorphism in size may be the consequence of trade-offs between the relationship between fecundity and size, the relationship between territory size and fish size and the cost of large size.

Wyllie Echeverria (1986) developed arguments that the relatively large size of pectoral fins and eyes of males of the four species she studied are compensation for reduced size. These relatively large parts could aid males in competing with females for food.

We found that six measurements are relatively large for males. These measurements may be related to feeding ability. The maximum size of dietary items probably is related to length of upper jaw, head length and perhaps interorbital width. The width of the orbit probably is related to the ability to detect food items. Swimming ability, particularly the ability to maneuver for capturing food, is probably related to length of the pectoral fin ray and perhaps the largest dorsal spine. Hobson & Chess (1978) argue that long fin spines found in some planktivores provide a defense against predation when feeding in the water column.

For some species, e.g. *S. entomelas, S. ovalis* and *S. rufus*, there is considerable dimorphism in size, but no or only one significant sexually dimorphic character. Conversely *S. ruberrimus* is not dimorphic in size, but male interorbital width, upper jaw length and dorsal spine length are relatively large. Thus it appears that sexually dimorphic characters in rockfish are related to factors other than or in addition to compensation for reduced size of males.

Perhaps the dimorphisms are related to either male mating behavior and/or territorial behavior. Fins are parts of aggressive displays. Relatively large fins and eyes tend to make a fish look larger than it really is. Rockfish have been observed in combat on rare occasions in which the combatants are mouth-locked. Haaker (1978) observed one combatant partially swallowing another. This behavior suggests that large head parts would tend to aid males in territorial behavior for species in which males are territorial. The courtship behavior observed by Helvey (1982) and Shinomiya & Ezaki (1991) suggests that the six relatively large parts could cause subtle advantages in courtship.

In summary the observed differences in dimorphisms in morphometric measurements may be related to compensation in feeding ability for reduced SL of males and territorial and mating behavior.

We believe that further research on sexual dimorphisms of rockfish would be fruitful. While we are confident that the trends we have noted are valid, it would be desirable to increase the sample size of some of the species in our study. It would also be interesting to verify that the trends we observe extend to other species of rockfish. More behavior studies on nearshore species should lead to a better understanding of the factors related to sexually dimorphic characters.

As we observed in the Introduction, sexual dimorphism is a very interesting subject and explanations for causes appear to be complex. While we do not expect final explanations to be developed soon, we do expect that pursuit of the explanations will lead to a better understanding of factors that affect the life history and population dynamics of rockfish.

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References cited

Boehlert, G.W. 1980. Size composition, age composition, and growth of canary rockfish, *Sebastes pinniger*, and splitnose rockfish, *S. diploproa*, from the 1977 rockfish survey. Mar. Fish. Rev. 42: 57–63.

Chen, L.C. 1971. Systematics, variation, distribution and biology of rockfishes of the subgenus *Sebastomus* (Pisces, Scorpaenidae, *Sebastes*). Bull. Scripps Inst. Oceanogr. Univ. Calif. 18. 115 pp.

Chen, L.C. 1986. Meristic variation in *Sebastes* (Scorpaenidae), with an analysis of character association and bilateral pattern and their significance in species seperation. NOAA Tech. Rep. NMFS. 45. 17 pp.

Darwin, C. 1871. The descent of man, and selection in relation to sex. Murray, London. 705 pp.

Dixon, W.J. & F.J. Massey, Jr. 1957. Introduction to statistical analysis. McGraw-Hill, New York. 488 pp.

Fraidenburg, M.R. 1980. Yellowtail rockfish, *Sebastes flavidus*, length and age composition off California, Oregon, and Washington in 1977. Mar. Fish. Rev. 42: 54–56.

Haaker, P.L. 1978. Observations of agonistic behavior in the treefish, *Sebastes serriceps* (Scorpaenidae). Calif. Fish and Game. 64: 227–228.

Hallacher, L.E. 1977. Patterns of space and food use by inshore rockfishes (Scorpaenidae: *Sebastes*) of Carmel Bay, California. Ph.D. Dissertation, University of California, Berkeley. 119 pp.

Helvey, M. 1982. First observations of courtship behavior in rockfish, genus *Sebastes*. Copeia 1982: 763–770.

Hobson, E.S. & J.R. Chess. 1978. Trophic relationships among fishes and plankton in the lagoon at Enewetak Atoll, Marshall Islands. U.S. Fish. Bull. 76: 133–153.

Holt, S.J. 1959. Report of the international training center on the methodology and techniques of research on mackerel (Rastrelliger). FAO/ETAP Rep. 1095. 120 pp.

Kleinbaum, D.G. & L.L. Kupper. 1978. Applied regression analysis and other multivariable methods. Duxbury Press, North Scituate. 556 pp.

Larson, R.J. 1980. Competition, habitat selection, and the bathymetric segregation of two rockfish (*Sebastes*) species. Ecol. Monogr. 50: 221–239.

Lenarz, W.H. 1980. Shortbelly rockfish, *Sebastes jordani*: a large unfished resource in waters off California. Mar. Fish. Rev. 42: 34–40.

Lenarz, W.H. 1987. Ageing and growth of widow rockfish. pp. 31–35. *In:* W.H. Lenarz & D.R. Gunderson (ed.) Widow Rockfish, Proceedings of a Workshop, Tiburon, Dec. 11–12, 1980, NOAA Tech. Rep. NMFS 48.

Lewin, R. 1988. Why is the world full of large females? Science 240: 884.

Love, M.S., M.H. Carr & L.J. Haldorson. 1991. The ecology of substrate-associated juveniles of the genus *Sebastes*. Env. Biol. Fish. 30: 225–243.

Love, M.S., P. Morris, M. McCrae & R. Collins. 1989. Life history aspects of 19 rockfish species (Scorpaenidae: *Sebastes*) from the Southern California Bight. NOAA Tech. Rep. (in press).

Love, M.S. & W.V. Westphal. 1981. Growth, reproduction, and food habits of olive rockfish, *Sebastes serranoides*, off central California. U.S. Fish. Bull. 79: 533–545.

Miller, D.J. & J.J. Geibel. 1973. Summary of blue rockfish and lingcod life histories; a reef ecology study, and giant kelp, *Macrocystis pyrifera*, experiments in Monterey Bay, California. Calif. Dept. Fish Game, Fish Bull. 158. 137 pp.

Moser, H.G. 1967. Reproduction and development of *Sebastodes paucispinis* and comparisons with other rockfishes off southern California. Copeia 1967: 773–797.

Murray, B.G., Jr. 1984. A climographic theory on the evolution of mating systems as exemplified by birds. pp. 71–140. *In:* M.K. Hecht, B. Wallace & G.T. Prance (ed.) Evolutionary Biology, Vol. 18, Plenum Press, New York.

Nelson,B. & T.J. Quinn, II. 1987. Population parameters for rougheye rockfish (*Sebastes aleutianus*). pp. 209–228. *In:* Proc. Int. Rockfish Symp., Anchorage, University of Alaska Sea Grant Rep. 87–2.

O'Connell, V.M. & F.C. Funk. 1987. Age and growth of yelloweye rockfish (*Sebastes ruberrimus*) landed in southeastern Alaska, pp. 171–185. *In:* Proc. Int. Rockfish Symp., Anchorage, University of Alaska Sea Grant Rep. 87–2.

Phillips, J.B. 1957. A review of the rockfishes of California (family Scorpaenidae). Calif. Dept. Fish & Game, Fish Bull. 104. 158 pp.

Seeb, L.W. 1986. Biochemical systematics and evolution of the scorpaenid genus *Sebastes*. Ph.D. Dissertation, University of Washington, Seattle. 176 pp.

Shine, R.S. 1988. The evolution of large body size in females: a critique of Darwins 'fecundity advantage' model. Amer. Nat. 131: 124–131.

Shinomiya, A. & O. Ezaki. 1991. Mating habits of the rockfish, *Sebastes inermis*. Env. Biol. Fish. 30: 15–22.

Six, L.D. & H.F. Horton. 1977. Analysis of age determination methods for yellowtail rockfish, canary rockfish, and black rockfish off Oregon. U.S. Fish. Bull. 75: 405–414.

Wilkens, M.E. 1980. Size composition, age composition, and growth of chilipepper, *Sebastes goodei*, and bocaccio, *S. paucispinis*, from the 1977 rockfish survey. Mar. Fish. Rev. 42: 48–53.

Wilkens, M.E. & K.L. Weinberg. 1986. Results of a bottom trawl survey of Pacific ocean perch off Washington and Oregon during 1985. pp. 241–265. *In:* Proc. Int. Rockfish Symp. Anchorage, University of Alaska Sea Grant Rep. 87–2.

Wyllie Echeverria, T. 1986. Sexual dimorphism in four species of rockfish genus *Sebastes* (Scorpaenidae). Env. Biol. Fish. 15: 181–190.

Wyllie Echeverria, T. 1987. Thirty-four species of California rockfishes: maturity and seasonality of reproduction. U.S. Fish. Bull. 85: 229–250.

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DEPTH DISTRIBUTIONS OF LATE LARVAE AND PELAGIC JUVENILES OF SOME FISHES OF THE CALIFORNIA CURRENT

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ABSTRACT

The vertical distribution of pelagic young-of-the-year larval and juvenile fishes in the California Current is reviewed. New data from synoptic midwater trawls conducted at depths of 13, 37, and 117 m along the central California coast are presented. Data for 15 species of rockfish, Dover and rex soles, northern anchovy, and Pacific whiting show that most species tend toward a uniform distribution among the three sampled depths. Notable exceptions include bocaccio (most abundant at 13 m) and blue, yellowtail, and pygmy rockfishes (most abundant at 117 m). With the advent of persistent upwelling during May and June, pelagic juvenile rockfish tend to occur deeper in the water column than in March–April. Data about shortbelly rockfish support the view that during periods of intense upwelling (May–June) relatively small fish stay deep, presumably to avoid advection offshore. There was not a clear relationship between depth distribution of fish and depth of the thermocline.

RESUMEN

Se revee la distribución vertical de larvas y juveniles de peces nacidos en el año en la Corriente de California. Se presentan datos nuevos de estudios sinópticos con redes de arrastre conducidos a profundidades de 13, 37, y 117 m a lo largo de la costa de California central. Datos de 15 especies de rocotes (*Sebastes* spp.), lenguados como *Microstomus pacificus* y *Glyptocephalus zachirus*, anchoveta norteña (*Engraulis mordax*), y merluza del Pacífico (*Merluccius productus*) demuestran que la mayoría de las especies tienen distribución uniforme entre las tres profundidades muestreadas. Excepciones notables incluyen *Sebastes paucispinis* (más abundante a 13 m) y *S. mystinus*, *S. flavidus*, y *S. wilsoni* (más abundantes a 117 m). Debido a la persistente surgencia de aguas, los juveniles pelágicos de rocotes tienden a ocurrir a mayores profundidades en la columna de agua durante mayo y junio que en marzo y abril. Datos sobre *S. jordani* apoya la noción que los peces pequeños se mantienen a profundidad durante períodos de intensa surgencia, presumiblemente tratando de evitar transporte hacia mar abierto. No se encontró una clara relación entre la distribución por profundidad de los peces y la profundidad de la termoclina.

INTRODUCTION

Knowledge of the vertical distribution of pelagic early life stages of fish is needed to understand transport and biological processes. Fish may adapt their behavior to take advantage of vertical shears in currents that might either retain the fish in or transport them to favorable areas (Bakun 1986; Sinclair 1988). After reviewing pertinent literature, we present results on the vertical distribution of rockfish (*Sebastes* spp.) and other species from our surveys of pelagic young-of-the-year rockfish off the coast of California from Monterey to Point Reyes.

Small rockfish larvae, which are only identified to genus because diagnostic characteristics are not known for most species, have generally been found at relatively shallow depths. Ahlstrom (1959) published the most detailed study on rockfish larvae off the coast of southern and Baja California. The larvae were found mostly in the upper mixed layer and thermocline. All but 3% of the rockfish larvae were collected in strata shallower than 80 m. Moser and Boehlert (1991) obtained similar results at two stations off southern California. Both studies indicated that the depth distribution of rockfish larvae is directly related to the depth of the thermocline. Rockfish larvae were found even shallower off Oregon (Richardson and Pearcy 1977; Boehlert et al. 1985). Barnett et al. (1984) found rockfish larvae in the neuston layer off southern California; Shenker (1988) found them in the neuston layer off Oregon. The data collected off southern California indicated that larvae were more abundant in the water column than in the neuston and epibenthic layers.

Ahlstrom (1959) found Pacific whiting (*Merluccius productus*) larvae deeper than rockfish and usually within or below the thermocline. Only 5% of the whiting were caught above 43 m, whereas 56% of the rockfish larvae were taken there.

Northern anchovy (*Engraulis mordax*) larvae are found at very shallow depths. For a 1959 study, Ahlstrom caught about 48% of anchovy between the surface and 48 m; less than 1% came from deeper than 88 m. Boehlert et al. (1985) did not catch any anchovy larvae deeper than 10 m. Shenker (1988) caught anchovy larvae in the neuston layer off Oregon. Barnett et al. (1984) tended to catch more anchovy larvae in the water column than in the neuston and epibenthic layers off southern California.

Larvae of the two species of flatfish in our study differ in their depth distribution. Pearcy et al. (1977) found that almost all Dover sole (*Microstomus pacificus*) larvae occurred in the upper 600 m of water off Oregon. Best catch rates were made in the 0–50-m depth stratum, but high rates also occurred in the 100–150-m stratum. Boehlert et al. (1985) caught rex sole (*Glyptocephalus zachirus*) larvae between the surface and 30 m; the highest catches occurred between 10 and 20 m. Shenker (1988) caught rex sole larvae in the neuston layer off Oregon.

Juveniles of several species of rockfish, including splitnose (*S. diploproa*) and bocaccio (*S. paucispinis*), have been captured at the surface associated with drifting kelp (Mitchell and Hunter 1970; Boehlert 1977). Shenker (1988) captured unidentified juvenile rockfish and juvenile black (*S. melanops*), blue (*S. mystinus*), and canary (*S. pinniger*) rockfish in the neuston layer. Juveniles of many species of rockfish have been captured with midwater trawls and purse seines in the upper 100 m (Brodeur and Pearcy 1986; Kendall and Lenarz 1987, and papers reviewed by them), but the vertical distribution of these species in the upper water column has not been published. Moser and Ahlstrom (1978) found juvenile blackgill rockfish (*S. melanostomus*), and a few other species that we rarely capture in our surveys, between 200 and 250 m.

METHODS

We collected juvenile fish at night with a modified Cobb midwater trawl off the coast between Monterey (36°35′N) and Point Reyes (38°10′N). The net, which is described by Wyllie Echeverria et al. (1990), nominally has a square mouth, but acoustic measurements showed that although the height of the mouth was 14 m, the width varied from 8 m (when the center of the net was at 13-m depth) to 13.5 m (at 117-m depth).

Acoustic measurements also showed that the net was not always at targeted depths, but precision was sufficient to separate tows taken at different targeted depths. We assume here that all tows were at their targeted depths. During the survey the targeted depth was usually 37 m but was set at 13 m for shallow stations. When time and depth allowed we towed at 13 m, 37 m, and 117 m to obtain data on the vertical distribution of fish. Since we did not use an opening-closing net, some contamination by specimens from nontargeted depths was possible. The net was dropped to the targeted depth as rapidly as possible while the vessel maintained steerage, was towed for 15 minutes at about 5 km per hour, and was then retrieved as rapidly as possible while the vessel maintained steerage. We do not believe that contamination is a serious problem. We used a cod end with 9.5-mm stretched mesh width that retained only some of the largest larvae and did not retain all of the smaller juveniles encountered. We did most of the work from mid-May through June, and from late March through mid-April, between 1983 and 1990.

We standardized catches for net mouth width by dividing by the width. For each station with tows at 13, 37, and 117 m, we calculated average depth for each captured species. We calculated average depths both as simple averages of individual station averages (unweighted) and from the sums of catches made at each depth over all stations (weighted). If the fish were equally abundant at the three sampled depths, the average depth would be 55.7 m. If the fish and samples were evenly distributed between 0 and 117 m, the average depth would be 58.5 m. Thus under the even-fish-distribution assumption, the uneven depth distribution of our samples had little effect on our estimates of average depth between the surface and 117 m. However, if there were relatively high densities of fish in unsampled strata, our estimates of average depth could be biased. We tested null hypotheses that catch rates for two depths were equal by using the paired *t* test and the sign test (Dixon and Massey 1957).

RESULTS

Results are presented for 15 species of rockfish — bocaccio, darkblotched rockfish (*S. crameri*), bank rockfish (*S. rufus*), black rockfish, shortbelly rockfish (*S. jordani*), squarespot rockfish (*S. hopkinsi*), canary rockfish, stripetail rockfish (*S. saxicola*), chilipepper (*S. goodei*), halfbanded rockfish (*S. semicinctus*), yellowtail rockfish (*S. flavidus*), brown rockfish (*S. auriculatus*), widow rockfish (*S. entomelas*), blue rockfish, and pygmy rockfish (*S. wilsoni*); 2 species of flatfish — Dover and rex sole; Pacific whiting; and northern anchovy (table 1). We also caught Pacific and speckled sanddabs (*Citharichthys sordidus* and *C. stigmaeus*), but the depth distribution data on these two species are being used for a thesis by graduate student Keith Sakuma at San Francisco State University and are not included in this paper. We collected at least one specimen at 61 stations with tows at 13, 37, and 117 m; 83 stations with tows at 13

TABLE 1
Number of Positive Stations, Average Depth (m) and Standard Error of the Average Depth for Pelagic Young-of-the-Year Fish off Central California during May–June

Species	Number of stations	Unweighted Average depth	Unweighted Standard error	Weighted Average depth	Weighted Standard error
Bocaccio	29	30.4	3.0	26.2	3.6
Darkblotched rockfish	9	33.7	11.7	24.7	5.3
Dover sole	10	39.0	11.8	28.8	9.1
Northern anchovy	9	41.8	12.2	25.0	17.8
Bank rockfish	4	52.3	26.5	15.4	12.1
Black rockfish	7	53.0	18.4	43.9	21.7
Shortbelly rockfish	43	53.6	5.0	36.2	8.2
Squarespot rockfish	27	54.7	7.6	39.4	27.6
Pacific whiting	59	54.8	3.3	27.8	9.1
Canary rockfish	20	55.2	6.2	80.3	38.3
Stripetail rockfish	11	56.9	6.5	51.1	17.6
Chilipepper	22	58.5	8.6	39.1	10.9
Halfbanded rockfish	5	60.5	17.6	40.7	32.3
Rex sole	24	63.5	7.4	42.5	6.7
Yellowtail rockfish	21	64.8	9.1	66.2	18.4
Brown rockfish	5	69.0	21.9	60.2	28.4
Widow rockfish	31	70.2	7.0	45.6	14.1
Blue rockfish	30	82.0	7.3	57.8	20.9
Pygmy rockfish	13	83.0	13.4	75.9	23.5
Average		56.7	10.8	43.5	17.1

Weighted averages are weighted by catches. Species are arranged by unweighted average depth.

and 37 m; 77 stations with tows at 37 and 117 m; and 64 stations with tows at 13 and 117 m. We captured more than 150,000 rockfish, 125,000 Pacific whiting, 1,250 northern anchovy, and 500 flatfish.

The unweighted average depth of most species was close to the average expected (55.7 m) when densities are equally distributed at the three sampled depths (table 1 and figure 1). The unweighted average over all species was 56.7 m. Weighted average depths were shallower than the unweighted averages for 17 of the 19 species. The average over species of weighted average depths was 13 m less than the unweighted average. Very large catches tended to occur at shallow depths. Weighted standard errors were about 50% greater than unweighted.

The results indicate that bocaccio were more common at shallow than at deep depths; densities of canary and halfbanded rockfish were lower at 13 m than at 37 m; and yellowtail, blue, and pygmy rockfish were most abundant at 117 m (table 2 and figure 2). Weighted 13-m densities of Pacific whiting were greater than 37-m densities, but the converse was true for unweighted densities. Catch rates of Pacific whiting appeared to be lowest at 117 m. Weighted and unweighted depth comparisons differed for widow rockfish.

There is evidence that average depth changes as the season progresses. We compared average depth in March and April with May and June for bocaccio, chilipepper, and blue, shortbelly, and widow rockfish in 1987, 1988, and 1990. Our data were insufficient to make such comparisons for other species. Unweighted average depth between the two time periods increased in all cases except for bocaccio in

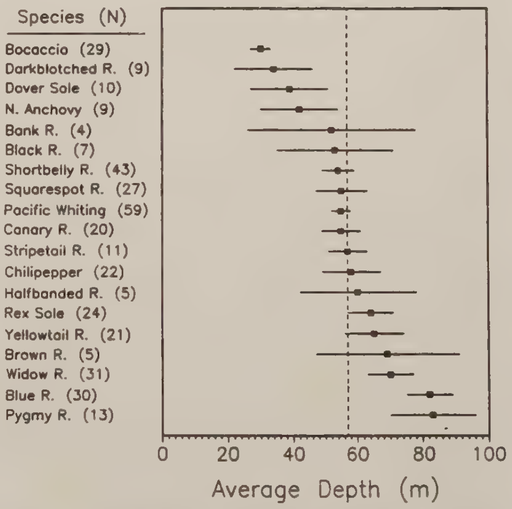

Figure 1. Unweighted average depths (*solid squares*), standard errors (*horizontal lines*), and number of stations with at least one positive tow at 13, 37, or 117 m (N) for pelagic young-of-the-year off central California during May–June. The overall average is shown as a *dashed vertical line*. (R. = rockfish)

TABLE 2

Results of Sign and Paired *t*-Tests That Catch Rates of Young-of-the-Year Fish Are Independent of Depth of Tow off Central California during May–June

	Probability of greater difference due to chance alone								
	13 and 37 m			37 and 117 m			13 and 117 m		
Species	*n*	Sign	*t*	*n*	Sign	*t*	*n*	Sign	*t*
Bocaccio	31	<0.10	>0.10	22	<0.01	<0.01	12	<0.05	<0.01
Darkblotched rockfish	12	>0.10	>0.10	5	>0.10	>0.10	6	>0.10	<0.05
Dover sole	11	>0.10	>0.10	9	>0.10	>0.10	8	>0.10	>0.10
Northern anchovy	14	>0.10	>0.10	12	>0.10	>0.10	3	>0.10	>0.10
Bank rockfish	6	>0.10	>0.10	4	>0.10	>0.10	4	>0.10	>0.10
Black rockfish	12	>0.10	<0.10	7	>0.10	>0.10	4	>0.10	>0.10
Shortbelly rockfish	63	>0.10	>0.10	53	>0.10	<0.10	40	>0.10	>0.10
Squarespot rockfish	26	>0.10	>0.10	30	>0.10	>0.10	24	>0.10	>0.10
Pacific whiting	73	<0.10	<0.01	68	<0.05	>0.10	58	>0.10	<0.05
Canary rockfish	19	<0.05	<0.05	16	<0.10	>0.10	6	>0.10	>0.10
Stripetail rockfish	14	>0.10	>0.10	11	>0.10	>0.10	6	>0.10	>0.10
Chilipepper	27	>0.10	>0.10	29	>0.10	>0.10	14	>0.10	>0.10
Halfbanded rockfish	9	<0.05	<0.10	6	>0.10	>0.10	3	>0.10	>0.10
Rex sole	26	>0.10	>0.10	30	>0.10	>0.10	24	>0.10	>0.10
Yellowtail rockfish	29	>0.10	>0.10	23	<0.10	<0.10	15	>0.10	>0.10
Brown rockfish	5	>0.10	>0.10	11	>0.10	>0.10	—	—	—
Widow rockfish	35	>0.10	>0.10	32	<0.10	<0.05	31	<0.10	<0.10
Blue rockfish	33	>0.10	>0.10	36	>0.10	<0.10	32	<0.05	<0.10
Pygmy rockfish	6	>0.10	>0.10	13	<0.10	<0.05	12	>0.10	>0.10

Results with probabilities less than 0.10 are underlined. *n* is the number of positive stations. Cases with fewer than three positive stations are not included.

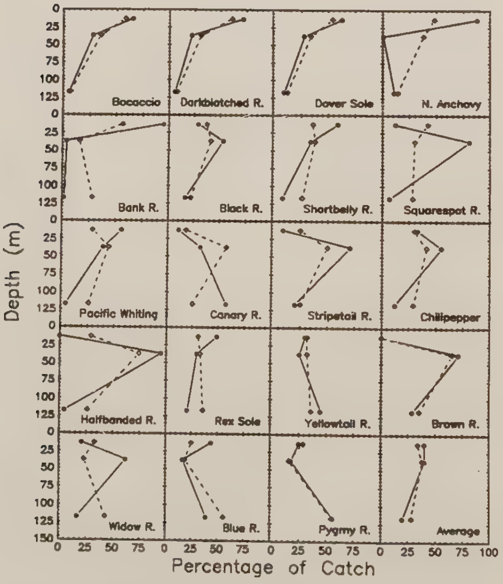

Figure 2. Weighted (*solid circles and lines*) and unweighted (*open diamonds and dashed lines*) depth distributions for pelagic young-of-the-year fish off central California during May–June. (R. = rockfish)

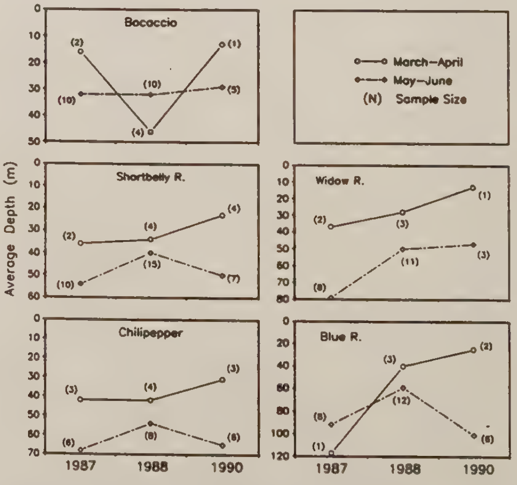

Figure 3. Unweighted average depths for pelagic young-of-the-year bocaccio, chilipepper, and shortbelly, widow, and blue rockfish off central California during March–April and May–June. Sample size is the number of stations with at least one positive tow at 13, 37, or 117 m. (R. = rockfish)

1988 and blue rockfish in 1987 (figure 3). Catches of these five species at 117 m were typically quite low in March–April. Similar results were obtained for weighted average depths. The unweighted overall average depth increased 19 m between the two periods, and weighted average increased 9 m.

Data were also available to compare size compositions of shortbelly rockfish in paired 13- and 37-m tows from 1987–90, and from unpaired 13- and 37-

m tows in 1987 and 1988. During May–June, small shortbelly rockfish (<50 mm) tended to be deeper than larger fish (figure 4). This was true both when the data were unweighted, as in the figure, or weighted by catch.

DISCUSSION

The vertical distribution of late larval and juvenile rockfish that we found in March–April is similar to that of rockfish larvae (Ahlstrom 1959; Richardson and Pearcy 1977; Boehlert et al. 1985; Moser and Boehlert 1991). Our catches were relatively low in tows deeper than 37 m. By May–June the average depth of capture increased by 9–19 m, and catch rates for 117-m tows were seldom significantly less than rates for shallow tows (table 2 and figure 2). Also, reported distributions of larval northern anchovy (Ahlstrom 1959; Boehlert et al. 1985) and rex sole (Boehlert et al. 1985) were shallower than we found for young-of-the-year of the same species in May–June. In contrast, our May–June catch rates for juvenile Pacific whiting indicated greater relative abundance at shallow depths than was reported for larvae by Ahlstrom (1959).

Perhaps the different pattern for Pacific whiting is related to their habit of spawning at depths of 130–500 m in midwater, up to 400 km off the coast (Bailey et al. 1982). Except for northern anchovy, the other species spawn relatively close to shore. Northern anchovy spawn at midwater (sometimes far offshore) in fairly shallow depths. Bailey et al. (1982) present data showing that large catches of Pacific whiting eggs and larvae often occur in areas where northward geostrophic flow at 200 m would tend to advect the fish onshore.

The young-of-the-year fish in our study inhabit a greater depth range in the water column than other investigators found for earlier life stages. The larger fish that characterize our samples may be adapted to searching the water column for optimal feeding conditions, low predation rates, or favorable currents, while the smaller fish tend to occupy depths that, on the average, are favorable. We found that, even though shortbelly rockfish tend to be closer to the surface in March–April than in May–June, the smaller fish were often deeper than the larger fish in May–June. Offshore transport of surface waters due to upwelling is more prevalent in May–June than in March–April. Perhaps the smaller fish are adapted to avoid the surface waters, and thus reduce the risk of offshore advection, during May–June.

We often found bocaccio at very shallow depths in May–June. Bocaccio grow very rapidly compared to other rockfish and can reach 20 cm in their first year (Phillips 1964). In order to realize their rapid growth, very young bocaccio may need to remain in the upper water column to encounter higher temperatures and food densities. The time spent in the upper water column may subject them to increased offshore advection. Other studies indicate that such advection may occur, because larvae of bocaccio are found farther offshore than the more abundant larvae of shortbelly rockfish (MacGregor 1986; Moser and Boehlert 1991).

Depth distributions were often shallower when observations were weighted by catches than when not weighted (tables 1 and 2 and figure 2). This was because very large catches tended to occur at shallow depths. It is possible that the fish school when at shallow depths, or avoid shallow depths unless con-

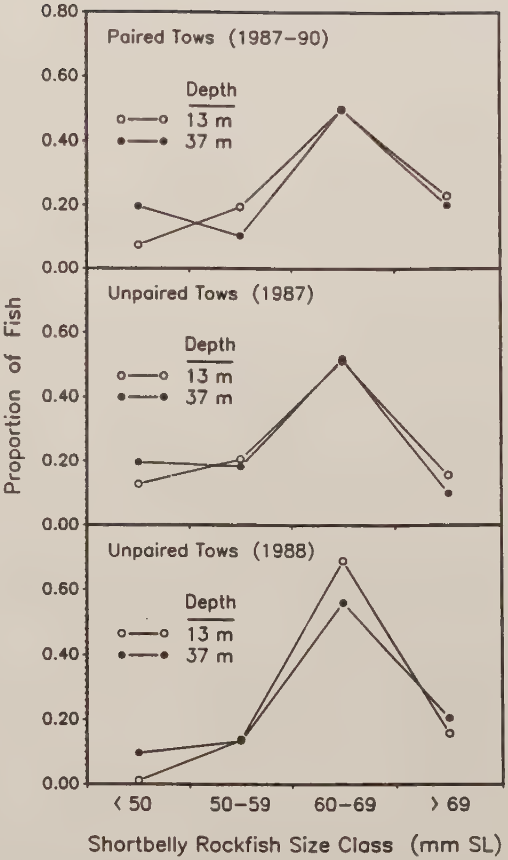

Figure 4. Size class compositions unweighted by catch for pelagic young-of-the-year shortbelly rockfish off central California dunng May–June.

ditions are particularly advantageous. Attempts to relate depth distributions at individual stations to oceanographic conditions have not produced convincing results. We did not find a clear relationship between depth distribution and the depth of the thermocline, as Ahlstrom (1959) and Moser and Boehlert (1991) found for rockfish larvae. However, large catches of juveniles often occur near to and offshore of upwelling fronts. We will continue to explore these relationships.

LITERATURE CITED

Ahlstrom, E. H. 1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish. Bull. 60:107–146.

Bailey, K. M., R. C. Francis, and P. R. Stevens. 1982. The life history and fishery of Pacific whiting, *Merluccius productus*. Calif. Coop. Oceanic Fish. Invest. Rep. 23:81–98.

Bakun, A. 1986. Local retention of planktonic early life stages tropical reef/bank demersal systems: the role of vertically-structured hydrodynamic processes? *In* Papers presented to the IREP (OSLR) workshop on recruitment in tropical demersal communities, D. Pauly and A. Yanez-Arancibia, eds. IOC Workshop Report 40 (Supplement), UNESCO, Paris, 15–32.

Barnett, A. M., A. E. Jahn, P. D. Sertic, and W. Watson. 1984. Distribution of ichthyoplankton off San Onofre, California, and methods for sampling very shallow coastal waters. U.S. Fish. Bull. 82:97–111.

Boehlert, G. W. 1977. Timing of the surface-to-benthic migration in juvenile rockfish, *Sebastes diploproa*, off southern California. U.S. Fish. Bull. 75:887–890.

Boehlert, G. W., D. M. Gadomski, and B. C. Mundy. 1985. Vertical distribution of ichthyoplankton off the Oregon coast in spring and summer months. U.S. Fish Bull. 83:611–621.

Brodeur, R. D., and W. G. Pearcy. 1986. Distribution and relative abundance of pelagic nonsalmonid nekton off Oregon and Washington, 1979–1984. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 46, 85 pp.

Dixon, W. J., and F. J. Massey, Jr. 1957. Introduction to statistical analysis, 2nd ed. New York: McGraw-Hill, 488 pp.

Kendall, A. W., Jr., and W. H. Lenarz. 1987. Status of early life history studies of northeast Pacific rockfishes. *In* Proceedings of the International Rockfish Symposium, Anchorage, Alaska. Univ. Alaska, Alaska Sea Grant Rep. 87–2, pp. 99–128.

MacGregor, J. S. 1986. Relative abundance of four species of *Sebastes* off California. Calif. Coop. Oceanic Fish. Invest. Rep. 27:121–135.

Mitchell, C. T., and J. R. Hunter. 1970. Fishes associated with drifting kelp, *Macrocystis pyrifera*, off the coast of southern California and northern Baja California. Calif. Fish Game 56:288–297.

Moser, H. G., and E. H. Ahlstrom. 1978. Larvae and pelagic juveniles of blackgill rockfish, *Sebastes melanostomus*, taken in midwater trawls off southern California and Baja California. J. Fish. Res. Bd. Can. 35:981–996.

Moser, H. G., and G. W. Boehlert. 1991. Ecology of pelagic larvae and juveniles of the genus *Sebastes*. Environ. Biol. Fishes 30:203–224.

Pearcy, W. G., M. J. Hosie, and S. L. Richardson. 1977. Distribution and duration of pelagic life of larvae of Dover sole, *Microstomus pacificus*; rex sole, *Glyptocephalus zachirus*; and petrale sole, *Eopsetta jordani*, in waters off Oregon. U.S. Fish. Bull. 75:173–183.

Phillips, J. B. 1964. Life history studies on ten species of rockfish (Genus *Sebastodes*). Calif. Dept. Fish Game, Fish Bull. 126, 70 pp.

Richardson, S. L., and W. G. Pearcy. 1977. Coastal and oceanic fish larvae in an area of upwelling off Yaquina Bay, Oregon. U.S. Fish. Bull. 75:125–145.

Shenker, J. M. 1988. Oceanographic associations of neustonic larval and juvenile fishes and Dungeness crab megalopae off Oregon. U.S. Fish. Bull. 86:299–317.

Sinclair, M. 1988. Marine populations: an essay on population regulation and speciation. Seattle: Univ. of Wash. Press, 252 pp.

Wyllie Echeverria, T., W. H. Lenarz, and C. A. Reilly. 1990. Survey of the abundance and distribution of pelagic young-of-the-year rockfish, *Sebastes*, off central California. NOAA-TM-NMFS-SWFC-147, 125 pp.

Seasonal and Annual Variability in the Diet of California Sea Lions *Zalophus californianus* at San Nicolas Island, California, 1981-86

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California sea lions haul out and breed on islands along the Pacific coasts of southern and Baja California and in the Gulf of California. About half of all births occur in southern California waters (Fig. 1), principally at San Miguel and San Nicolas Islands (Stewart et al. In press). Some studies have shown that diet varies geographically, perhaps influenced by seasonal variability of various prey (Fiscus and Baines 1966, Ainley et al. 1982, Everitt et al. 1981, Hawes 1983, Antonelis et al. 1984, Aurioles et al. 1984, Antonelis et al. 1990, Lowry et al. 1990). Here we describe seasonal and annual variability in the diet of California sea lions that hauled out at San Nicolas Island from 1981 through 1986.

Methods

We collected sea lion scats every one or two months at several rookeries and hauling grounds at San Nicolas Island (Fig. 1). Scats were washed through nested sieves (mesh sizes of 2.8 mm, 1.5 mm, and 0.71 mm) to recover hard parts such as fish otoliths, cephalopod beaks (i.e., mandibles), shark teeth, and invertebrate exoskeletal fragments. We identified prey species by comparing those remains with museum and personal voucher collections.

The frequency of occurrence (FO) of each prey taxon was calculated as the proportion of scats in each sample that contained at least one hard part from a prey taxon. We pooled monthly samples into four groups: winter (December–February), spring (March–May), summer (June–August), and autumn (September–November). We tested the null hypotheses that frequencies of occurrence of the most common prey (those that occurred in 5% or more of all scats) did not differ among seasons nor among years using a two-way analysis of variance (Program 7D of BMDP-87; Dixon 1987); we excluded data for 1981 from this analysis because we lacked data for some seasons. We tested the null hypothesis that dietary diversity did not differ among seasons or among years using multiway contingency table analysis (Program 4F of BMDP-88; Dixon 1988).

Results

We examined 1232 scats from summer 1981 through autumn 1986; 1085 of those contained identifiable prey hard parts (Table 1). We identified 32 prey taxa to species and 6 to genus, but only two genera of cephalopods and five of fish occurred in 5% or more of the scats. Therefore, we confined our analyses of seasonal and annual variability in diet to the latter 7 taxa. Northern anchovy *Engraulis mordax* was the most common prey, occurring in about half (50.6%) of all scats; Pacific whiting *Merluccius productus*, jack mackerel *Trachurus symmetricus*, rockfish *Sebastes* spp., and market squid *Loligo opalescens* each occurred in about 22–30% of scats (Table 2).

We are limited in our generalizations about seasonal trends in the frequencies of occurrence of prey species because of strong seasonal-annual interactions (ANOVA, $P < 0.05$). There are, however, some differences apparent among some seasons and years (Fig. 2). Northern anchovy was eaten more often in winter than in other seasons in 1982, 1983, and 1984, but not in 1985 or 1986; anchovy was present in more than 60% of scats each season in 1986. Furthermore, anchovy occurred in scats more often from 1984 through 1986 than in earlier years. Pacific whiting was eaten frequently from summer 1981 through spring 1982, and in spring

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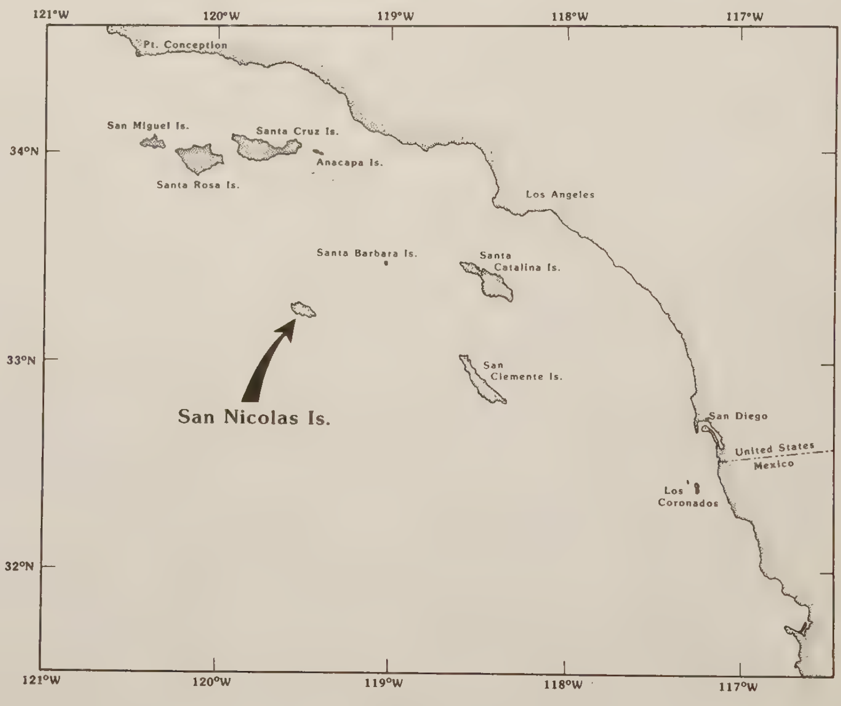
Fishery Bulletin, U.S. 89:331–336 (1991).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Los Angeles
Santa Barbara Is.
Santa Catalina Is.
San Clemente Is.
San Nicolas Is.
San Diego
United States
Mexico
Los Coronados

Figure 1

Map of Southern California Bight showing location of San Nicolas Island.

Table 1

Scat samples of *Zalophus californianus* collected at San Nicolas Island, California.

Year	Winter	Spring	Summer	Autumn	Total
1981	0	0	24	18	42
1982	12	15	68	13	108
1983	4	42	150	55	251
1984	75	35	107	93	310
1985	62	77	64	63	266
1986	35	24	80	116	255
Total	188	193	493	358	1232

1984 through spring 1985. Jack mackerel was found in scats more often in summer 1981 through autumn 1983 than after that period. Rockfish were commonly found in winter 1982, and spring 1984 through spring 1985. Market squid was more common in the diet prior to 1983 and its frequency of occurrence was higher in either autumn or winter, or both, each year except in 1984. Pelagic red crabs *Pleuroncodes planipes* appeared in scats in 1983, were frequently eaten through 1985, and then disappeared from the sea lions' diet. Pacific mackerel occurred frequently in summer and autumn 1982. *Octopus* spp. were eaten more often in spring 1984 than at any other time and appeared in the diet mostly in spring and summer of all years.

About 69% of all scats contained one or two prey taxa (Fig. 3). There were significant season-year interactions ($P<0.05$) for all years and seasons, but the number of prey taxa occurring in each scat was greatest from 1981 through 1984 and least in 1985 and 1986 (Fig. 3).

Discussion

California sea lions forage in a number of different habitats and depth strata in the Gulf of California and along the North American Pacific coast from Baja California to British Columbia. The composition of the sea lions' diet varies geographically (Jameson and

Table 2

Prey found in scat samples (*n*) and frequency of occurrence (expressed in %) for prey found in 1085 California sea lion scats collected at San Nicolas Island, California, 1981–86.

Prey			
Scientific name	Common name	*n*	%
Teleosts			
Engraulis mordax	northern anchovy	550	50.6
Merluccius productus	Pacific whiting	318	29.3
Trachurus symmetricus	jack mackerel	303	27.9
Sebastes spp.	rockfish	282	25.9
Scomber japonicus	Pacific (chub) mackerel	123	11.3
Chromis punctipinnis	blacksmith	22	1.9
Oxyjulis californica	señorita	15	1.3
Porichthys notatus	plainfin midshipman	5	0.4
Cololabis saira	Pacific saury	5	0.4
Icichthys lockingtoni	medusafish	5	0.4
Lycodes cortezianus	bigfin eelpout	4	0.3
Chilara taylori	spotted cusk-eel	3	0.2
Microstomus pacificus	dover sole	3	0.2
Citharichthys spp.	sanddab	3	0.2
Cymatogaster aggregata	shiner surfperch	3	0.2
Zalembius rosaceus	pink seaperch	3	0.2
Lyopsetta exilis	slender sole	2	0.2
Leuroglossus stilbius	California smoothtongue	2	0.1
Symbolophorus californiensis	California lanternfish	2	0.1
Sardinops sagax	Pacific sardine	2	0.1
Phanerodon furcatus	white seaperch	2	0.1
Zaniolepis spp.	combfish	2	0.1
Citharichthys sordidus	Pacific sanddab	2	0.1
Girella nigricans	opaleye	1	0.1
Medialuna californiensis	halfmoon	1	0.1
Argentina sialis	Pacific argentine	1	0.1
Stenobrachius leucopsarus	northern lampfish	1	0.1
Anoplopoma fimbria	sablefish	1	0.1
Icelinus tenuis	spotfin sculpin	1	0.1
Unid. Myctophidae	lanternfish	10	0.9
Unid. Embiotocidae	surfperch	3	0.2
	unid. fishes	72	6.6
	unid. flatfish	3	0.2
Elasmobranchs			
Prionace glauca	blue shark	1	0.1
Cephalopods			
Loligo opalescens	market squid	238	21.9
Octopus spp.	octopus	70	6.4
Onychoteuthis borealijaponicus	squid	52	4.7
Abraliopsis spp.	squid	24	2.2
Gonatus spp.	squid	18	1.6
Gonatopsis borealis	squid	13	1.1
Chiroteuthis calyx	squid	1	0.1
Unid. Gonatidae	squid	4	0.3
	unid. cephalopod	20	1.8
Crustaceans			
Pleuroncodes planipes	pelagic red crab	118	10.8
	unid. crustacean fragments	5	0.4
Algas			
Unid. Algae	algae	6	0.5

Kenyon 1977, Bowlby 1981, Everitt et al. 1981, Jones 1981, Bailey and Ainley 1982, Antonelis et al. 1984, Aurioles et al. 1984, Roffe and Mate 1984), but dietary diversity appears to be rather low in each location relative to the number of prey taxa consumed rangewide. Our studies of seasonal and annual variability in diet of sea lions at San Nicolas Island further support the classification of California sea lions as plastic specialists (Morse 1980). California sea lions exploit a few resources at a time, but prey composition of the diet is temporally dynamic; they capitalize on the more seasonally abundant and accessible schooling or aggregating prey.

The dietary occurrence of the sea lions' primary prey (northern anchovy, Pacific whiting, rockfish, jack mackerel, and market squid) appears to be related to the seasonal and annual occurrence of those prey species near San Nicolas Island. Market squid were eaten most often in autumn and winter in most years corresponding with the seasonal nearshore movements of spawning squid in this area (Bedford et al. 1983, Klingbeil 1986). Market squid were not commonly eaten by sea lions in 1983 and 1984, a time when squid were uncommon in the Southern California Bight (cf. Bedford et al. 1983; Klingbeil 1984, 1985, 1986; Grant 1987).

The presence of northern anchovy in the diet of sea lions seems to be related to the availability of anchovy near San Nicolas Island. Northern anchovy were uncommon near San Nicolas Island from 1982 through 1984, but were quite abundant in that area in 1985 and 1986 (Bindman 1986, Methot and Lo 1987). Sea lions consumed northern anchovy frequently in all seasons in 1985 and 1986, but substantially lower from 1981 through 1984, except during winter when anchovy were spawning and evidently nearer to San Nicolas Island than in other seasons.

The number of prey taxa eaten appears to be closely linked to the abundance and availability of northern anchovy. When anchovy were abundant near San Nicolas Island, sea lions evidently ate them in preference to other species. Both seasonal and annual patterns indicate that when the frequency of occurrence of anchovy in the diet is high, the number of prey species consumed is low. When northern anchovy are not available the breadth of the diet increased, with 3 to 4 other species being eaten.

Jack mackerel were displaced northward out of the Southern California Bight in 1984 when ocean surface currents changed and warm water associated with the 1982/83 El Niño-Southern Oscillation intruded into that area from Baja California (Mason 1989); the presence of jack mackerel in sea lion scats declined substantially then. Pelagic red crabs were transported into the Southern California Bight during this warm-water intrusion and they were frequently eaten by sea lions in 1983 and, to a lesser extent, through 1985 when they disappeared from their diet.

The dietary and behavioral flexibility of California sea lions in response to movements and availability of prey and to environmental perturbations (e.g., El Niño Southern Oscillation) may be one of the most important factors contributing to the consistent increase in their abundance during the past several decades. Relative to other locations, it appears that northern anchovy may be one of the most important prey of California sea lions near San Nicolas Island. This regional phenomenon is due to the proximity of San Nicolas Island to large spawning aggregations of northern anchovy compared with other locations where dietary studies of California sea lion have been made.

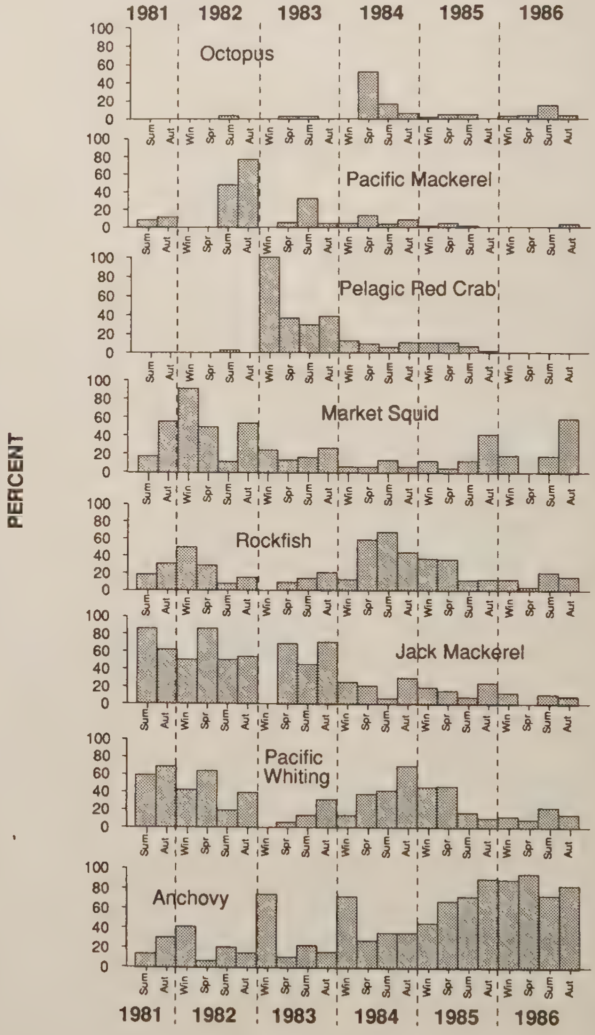

Figure 2

Seasonal frequency of occurrence (%) for eight prey taxa found in California sea lion scats collected at San Nicolas Island, California.

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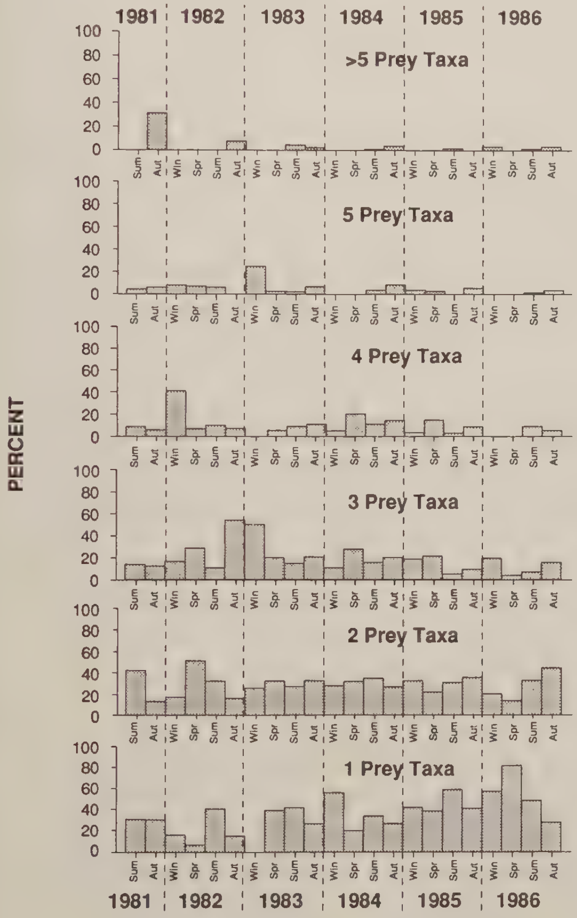


Figure 3

Frequency distributions of the numbers of prey taxa found in California sea lion scats collected at San Nicolas Island, California, summer 1981–autumn 1986.

Citations

Ainley, D.G., H.R. Huber, and K.M. Bailey
1982 Population fluctuations of California sea lions and the Pacific Whiting fishery off central California. Fish. Bull., U.S. 80:253–258.

Antonelis, G.A., C.H. Fiscus, and R.L. DeLong
1984 Spring and summer prey of California sea lions, *Zalophus californianus*, at San Miguel Island, California, 1978–1979. Fish. Bull., U.S. 82:67–76.

Antonelis, G.A., B.S. Stewart, and W.F. Perryman
1990 Foraging characteristics of northern fur seals (*Callorhinus ursinus*) and California sea lions (*Zalophus californianus*) in the waters around San Miguel Island, California. Can. J. Zool. 68: 150–158.

Aurioles, D., C. Fox, F. Sinsel, and G. Tanos
1984 Prey of the California sea lion (*Zalophus californianus*) in the Bay of La Paz, Baja California Sur, Mexico. J. Mammal. 65:519–521.

Bailey, K.M., and D.G. Ainley
1982 The dynamics of California sea lion predation on Pacific whiting. Fish. Res. (Amst.) 1:163–176.

Bedford, D., T. Jow, R. Klingbeil, R. Read, J. Spratt, and R. Warner
1983 Review of some California fisheries for 1982. Calif. Coop. Oceanic Fish. Invest. Rep. 24:6–10.

Bindman, A.G.
1986 The 1985 spawning biomass of the northern anchovy. Calif. Coop. Oceanic Fish. Invest. Rep. 27:16–24.

Bowlby, C.E.
1981 Feeding behavior of pinnipeds in the Klamath River, northern California. M.A. thesis, Humboldt State Univ., Arcata, CA, 74 p.

Dixon, W.J.
1987 BMDP 1987 IBM-PC Program Version. Manual edition: 1983, 1985 reprint. BMDP Statistical Software, Inc., 1440 Sepulveda Blvd., Los Angeles, CA 90025. Univ. Calif. Press, Berkeley.
1988 BMDP 1988 IBM-PC Program Version. Manual edition: 1988. BMDP Statistical Software, Inc., 1440 Sepulveda Blvd., Los Angeles, CA 90025. Univ. Calif. Press, Berkeley.

Everitt, R.D., P.J. Gearin, J.S. Skidmore, and R.L. DeLong
1981 Prey items of harbor seals and California sea lions in Puget Sound, Washington. Murrelet 62: 83–86.

Grant, J.
1987 Review of some California fisheries for 1986. Calif. Coop. Oceanic Fish. Invest. Rep. 28: 11–20.

Fiscus, C.H., and G.A. Baines
1966 Food and feeding behavior of Steller and California sea lions. J. Mammal. 47:195–200.

Hawes, S.D.
1983 An evaluation of California sea lion scat samples as indicators of prey importance. M.S. thesis, San Francisco State Univ., San Francisco, 50 p.

Jameson, R.J., and K.W. Kenyon
1977 Prey of sea lions in the Rogue River, Oregon. J. Mammal. 58:672.

Jones, R.E.
1981 Food habits of smaller marine mammals from northern California. Calif. Acad. Sci. Proc. 42: 409–433.

Klingbeil, R.
1984 Review of some California fisheries for 1983. Calif. Coop. Oceanic Fish. Invest. Rep. 25:7–15.
1985 Review of some California fisheries for 1984. Calif. Coop. Oceanic Fish. Invest. Rep. 26:9–16.
1986 Review of some California fisheries for 1985. Calif. Coop. Oceanic Fish. Invest. Rep. 27:7–15.

Lowry, M.S., C.W. Oliver, C. Macky, and J.B. Wexler
1990 Food habits of California sea lions *Zalophus californianus* at San Clemente Island, California, 1981–86. Fish. Bull., U.S. 88:509–521.

Mason, J.E.
1989 The southern California jack mackerel fishery, and the age and length composition of the catch for the 1972–73 through 1983–84 seasons. Calif. Dep. Fish Game, Mar. Res. Tech. Rep. 58, 38 p.

Methot, R.D., and N.C.H. Lo
1987 The spawning biomass of the northern anchovy in 1987. SWFC Admin. Rep. LJ-87-14, Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, P.O. Box 271, La Jolla, CA 92038-0271, 46 p.

Morse, D.H.
1980 Behavioral mechanisms in ecology. Harvard Univ. Press, Cambridge.

Roffe, T.J., and B.R. Mate
1984 Abundances and feeding habits of pinnipeds in the Rogue River, Oregon. J. Wildl. Manage. 48:1262–1274.

Stewart, B.S., P.K. Yochem, R.L. DeLong, and G.A. Antonelis
In press Status and trends in abundance of pinnipeds on the Southern California Channel Islands. *In* Hochberg, F.G. (ed.), Recent advances in California islands research. Proceedings, Third California islands symposium, Santa Barbara, CA. Bull. South Calif. Acad. Sci.

Southwest Fisheries Science Center
Tiburon Laboratory

National Marine Fisheries Service
Southwest Fisheries Science Center
Tiburon Laboratory
3150 Paradise Drive
Tiburon, CA 94920

Laboratory Objectives

The Tiburon Laboratory is a component of the National Marine Fisheries Service (NMFS), Southwest Fisheries Science Center. Its principal mission is to study groundfish life cycles, population dynamics, and fisheries.

Research at the Laboratory is divided into several investigations: Groundfish Analysis, Groundfish Communities, Groundfish Physiological Ecology, and Underutilized Resources. The Tiburon Laboratory also uses aquarium facilities at the University of California's Bodega Research Laboratory at Bodega Bay.

Personnel

Dr. Alec D. MacCall, Director
Dr. William H. Lenarz, Groundfish Analysis Investigation
Dr. Edmund S. Hobson, Groundfish Communities Investigation
Dr. Jeannette Whipple, Physiological Ecology Investigation
Susumu Kato, Trade and Industry Services

Areas of Expertise

The Groundfish Analysis Investigation provides stock assessments of rockfish (*Sebastes* spp.) to the Pacific Fishery Management Council. This Investigation also studies the causes of variability in recruitment and abundance of rockfish stocks, and is working to develop a capability to predict fluctuations. The latter functions involve annual midwater trawl surveys of juvenile rockfish abundance off central California, determination of birthdates from examination of daily rings on otoliths, and analysis of oceanographic processes and conditions.

OREGON
EUREKA
RENO
NEVADA
SACRAMENTO
TIBURON
OAKLAND
SAN FRANCISCO
PACIFIC OCEAN
CALIFORNIA
LAS VEGAS
LOS ANGELES

The mission of the Groundfish Communities Investigation is to study the effects of environmental change on the distribution, abundance, and recruitment of groundfish species, including regular seasonal transformations of habitat as well as changes associated with irregular environmental events such as El Niño. Emphasis is on how these changes affect interspecific relationships, particularly those between predators and prey. Information comes from nearshore underwater observations and collections with SCUBA, and also from bottom trawl and ROV operations in deep water. Personnel from this Investigation also study the life history and status of lingcod off California.

The Physiological Ecology Investigation is responsible for the assessment of the general physiological health of groundfish populations, and is developing an understanding of the relationships between physiological health and population productivity. This Investigation examines fish for caloric content, lipid content, gonadal development, and presence of disease and contaminants.

Fishery investigations that are not specifically associated with groundfish are conducted by a separate investigation under the Director's Office. This includes assessments of salmon runs from the Klamath and Sacramento rivers, studies in fisheries economics, and investigation of fisheries and resource issues surrounding dredge spoil disposal in the Gulf of the Farallons.

Susumu Kato, a fishery biologist associated with the Southwest Region of NMFS, researches uses of underutilized species at Tiburon Laboratory. Two recent projects include the devel-

The Tiburon Laboratory is located north of San Francisco on the west side of San Francisco Bay.

opment of a local hagfish fishery to produce leather products, and application of "bonesoftening" technique to shortbelly rockfish, *Sebastes jordani*, to improve use of this species as food.

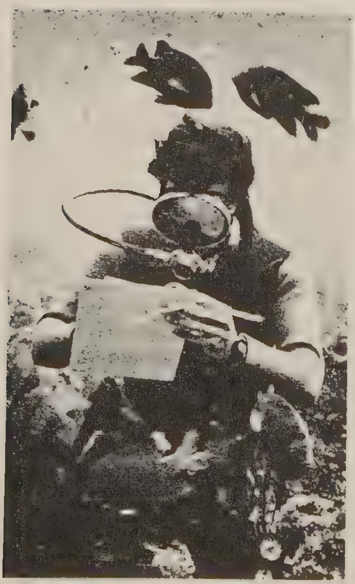
Laboratory Features

The Tiburon Laboratory is located on the largest bay-estuary system on the West Coast: San Francisco Bay. The Laboratory is only 6 miles from the Golden Gate, providing easy access to coastal waters and the continental shelf. The San Francisco metropolitan area is close, as are a number of major universities and colleges such as the University of California campuses at Berkeley, Davis, and Santa Cruz; California State University campuses at San Francisco, Hayward, San Jose, and Sonoma; and Stanford University in Palo Alto.

Laboratory History

In 1961 the Bureau of Sport Fisheries and Wildlife (Department of the Interior) established a Marine Sport Fish Laboratory at Tiburon. The Laboratory's small staff occupied one of the buildings on a large tract of government land. The site was formerly used as a codfish packing plant (1877–1904), as a coaling station by the U.S. Navy (1904–31), as a Maritime Academy (1931–40), and as an Anti Submarine Net Depot (1940–58.) The Sport Fish Laboratory carried out research on game fish migration and on the ecology and behavior of coastal fishes.

In 1970 the Laboratory was trans-



Tiburon Laboratory divers conduct rockfish population counts off the Sonoma and Mendocino County coastlines.

Southwest Fisheries Science Center's research vessel, *David Starr Jordan*.

ferred from the Department of the Interior to the Department of Commerce to join with a number of ocean-oriented federal agencies in the newly-established National Oceanic and Atmospheric Administration (NOAA) and became part of the National Marine Fisheries Service. Research efforts broadened to include studies on market fishes and their associated fisheries, as well as recreational fishes.

After the changeover to NOAA, the Tiburon Laboratory was initially a part of the NMFS Southwest Region based at Terminal Island, California, but in 1975 it became a component of the Southwest Fisheries Science Center, one of four regional research centers in the National Marine Fisheries Service. The Southwest Fisheries Science Center oversees research in laboratories at La Jolla, Honolulu, Monterey, and Tiburon. In 1975 the Tiburon Laboratory declared excess 35 unused acres and associated buildings, which were officially transferred to San Francisco State University in 1977. That property currently houses the University's Romberg Tiburon Centers, including the Tiburon Center for Environmental Studies.

As a result of the passage of the Fisheries Conservation and Management Act in 1976, increased emphasis was placed on research directly applicable to fisheries management. During the 1980s, the Tiburon Laboratory developed a coordinated multidisciplinary program focusing on the rockfishes and their fisheries. This program combines the strengths of progressive quantitative stock assessment methods with an ecosystem approach on one hand and a physiological ecology approach on the other. The result is to provide an exceptionally complete understanding on which to base management decisions.

Cooperating Agencies

Groundfish and salmon fishery research conducted by the Tiburon Laboratory benefits from cooperation with the California Department of Fish and Game, San Francisco State University, the University of California at Davis, and its Bodega Marine Laboratory. The Tiburon Laboratory's habitat and ecosystem research is conducted in collaboration with the University of Southern California, the University of Hawaii, the Gulf of the Farallones Marine Sanctuary, the U.S. Fish and Wildlife Service, the U.S. Army Corps of Engineers, and the Environmental Protection Agency. In addition, laboratory scientists work with independent academic groups such as the Point Reyes Bird Observatory, and with public interest, fishermen's and conservation organizations such as the Tyee Club.

Alec D. MacCall

9149

VARIATIONS IN THE CATCH OF JACK MACKEREL IN THE SOUTHERN CALIFORNIA PURSE SEINE FISHERY

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ABSTRACT

Jack mackerel landings from southern California sampled by the California Department of Fish and Game show a high degree of variability in recruitment success. The period from 1947 to 1983 is examined for variations in landings due to changes in fishing effort of the multispecies purse seine fishery. Fishing effort for jack mackerel has been affected by the availability of alternative species such as Pacific sardine and Pacific mackerel, and by economic factors including cannery capacity and the price of imported mackerel. Significant variations in recruitment success are apparent. Above-average recruitment for jack mackerel and Pacific mackerel, both pelagic species in southern California waters, often occurs in the same years.

The age composition of jack mackerel landings has changed noticeably during this period. Before 1965, fish three years old or older contributed significantly to the fishery, but after 1965 the fishery was dominated by one- and two-year-old fish. The seasonal nature of the multispecies fishery and the decreased contribution of older fish from the fall fishery are reflected in this change in age composition. Other factors include economic effects, the frequency of relatively strong year classes, shifts in the areas fished, and possible changes in fish behavior.

RESUMEN

Los desembarcos de la macarela (*Trachurus symmetricus*) del sur de California muestreada por el Departamento de Pesca y Caza de California muestra un alto grado de variabilidad en reclutamiento. Se examina el período de 1947 a 1983 con el fin de detectar variaciones en desembarco con respecto al esfuerzo de la pesquería de red de cerco multiespecífica. El esfuerzo de pesca de macarela ha sido afectado por la disponibilidad de especies alternativas como la sardina del Pacífico (*Sardinops sagax*) y la macarela del Pacífico (*Scomber japonicus*), y por factores económicos tales como la capacidad de las enlatadoras y el precio de la macarela importada. Se encontraron variaciones significativas en el éxito del reclutamiento. Reclutamiento por arriba del promedio de la macarela y la macarela del Pacífico, ambas especies pelágicas de las aguas del sur de California, ocurren a menudo en el mismo año.

La composición en edad de la macarela ha cambiado notablemente durante este período. Antes de 1965, peces de tres años de edad o mayores contribuían significativamente a la pesquería, pero después de 1965 la pesquería ha sido dominada por peces de uno y dos años. La estacionalidad de la pesquería multiespecífica y una menor contribución de los peces más viejos de la pesquería de otoño se reflejan en este cambio en composición de edad. Otros factores incluyen factores económicos, la frecuencia relativa de clases de edad fuertes, cambios en las áreas de pesca, y posibles cambios en el comportamiento de los peces.

INTRODUCTION

Jack mackerel, *Trachurus symmetricus*, has been an economically important species for the southern California purse seine fleet since 1947, averaging nearly $2 million in landings per year since 1947 (values not adjusted for inflation; MacCall et al. 1980). The population ranges from Baja California to the Gulf of Alaska and far offshore. MacCall and Stauffer (1983) estimated the total biomass to be 1.48 to 1.81 million MT. Most of the jack mackerel landed (over 90%) are caught by purse seiners in southern California waters, with smaller sporadic landings to the north at Monterey, California, and to the south at Ensenada, Mexico (MacCall et al. 1980). The purse seine (wetfish) fleet harvests jack mackerel from only a small portion of its range and captures only young fish.

Canneries started packing jack mackerel as a substitute for Pacific mackerel, *Scomber japonicus*, and Pacific sardine, *Sardinops sagax*, during the collapse of the sardine population and the decline of the Pacific mackerel population in the late 1940s (Roedel 1953). Jack mackerel are taken by the fleet from nearshore waters along the coast between Point Conception and the Mexican border, around islands in the

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[Manuscript received January 30, 1991.]

Southern California Bight, and offshore at Tanner and Cortez banks. Schools of mackerel are sometimes species specific, but often consist of a mixture of jack mackerel, Pacific mackerel, and Pacific sardine. The jack mackerel caught in the purse seine fishery are primarily small (about 100–350 mm fork length, FL) and young (0–5 years old). They are canned at Terminal Island and Port Hueneme for human consumption and pet food (MacCall et al. 1980).

Jack mackerel have been sampled by the California Department of Fish and Game at the Terminal Island canneries since 1947 (Knaggs 1974a). Length is measured; sex is recorded; and otoliths are removed for age determination. The validity of otolith age determinations for this population was examined by Knaggs and Sunada (1974), and maturation and growth were documented by Wine and Knaggs (1975).

The purposes of this paper are to review the factors that have affected the jack mackerel landings, examine the age composition of the catch, and look at the pattern of recruitment.

MULTISPECIES ASPECTS OF THE FISHERY

Large fluctuations in the volume of jack mackerel landings have resulted from a number of factors related to the variables present in a multispecies fishery. The southern California wetfish fleet developed in the 1930s to harvest Pacific sardine and Pacific mackerel, but took small amounts of jack mackerel (then called horse mackerel) incidentally to the target species. The history of the jack mackerel fishery up to 1951 was reviewed by Roedel (1953).

In the 1930s and 1940s Pacific sardine was by far the leading species landed by the fleet, with Pacific mackerel second (figure 1). Both Pacific mackerel and sardines were canned, but sardines commanded the highest price because they were also processed for fish oil and meal, and fish oil was in demand at that time. Canneries paid a much lower price for jack mackerel: in 1935 jack mackerel brought $6 per ton while Pacific mackerel brought $15 per ton. Northern California sardine landings declined in the mid-1940s, and many of the purse seiners went south, increasing the fishing pressure on Pacific mackerel and sardines in southern California waters (Fitch 1952). The sardine catch dropped in 1947 despite the increased effort, but revived briefly in southern California in 1949 and 1950 (figure 1).

In 1947, when Pacific mackerel and sardines became so scarce that fishermen could not fill the canneries' demands, large quantities of jack mackerel were first accepted. The name was changed from horse mackerel to jack mackerel in 1948 to enhance consumer appeal, and canneries developed a marketable product. The jack mackerel catch, therefore, did not increase gradually as the fishery developed, but started with nearly the highest landings ever recorded for the species.

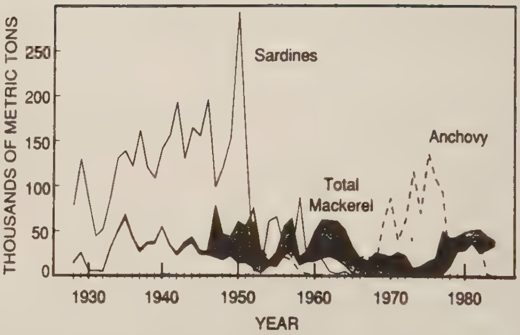

Figure 1. Annual landings of wetfish in southern California. Total mackerel comprises two species: Jack mackerel (*shaded area*) and Pacific mackerel (*area below shading*).

Northern anchovy, *Engraulis mordax*, has been an important species to the wetfish fleet since the beginning of the anchovy reduction fishery in late 1965. Within four years anchovy had topped jack mackerel landings and, except for 1978, continued to lead landings from 1969 to 1982 (Anon. 1984). Anchovy are fished by the same boats, but with nets with smaller mesh than the nets used for the other three species; so boats are not likely to fish for both anchovy and jack mackerel in the same trip. Anchovy are reduced to fish meal, but have a lower oil content than sardines. Anchovy do not command as high a price as jack mackerel, but fishing boats may shift between anchovy and jack mackerel when availability or marketability changes, or when the anchovy season opens or closes.

The fishing season for anchovy in southern California opens on September 15 and is limited to a quota on reduction landings. Fishing often starts a few weeks later, because the fishermen use the first few weeks of the season to negotiate prices with the canneries. Through 1978, the season closed on May 15 or as soon as the quota was filled. Since 1979, the closure date has been June 30, with an additional closed period on reduction landings in February and sometimes March. During the 1973 and 1974 seasons the increased cost of fuel kept boats nearer shore where jack mackerel could not be found, but anchovy were available. Anchovy fishing diverted effort away from jack mackerel fishing and contributed to reduced jack mackerel landings in 1973, 1974, 1977, and 1980 (Mason 1989).

The resurgence of Pacific mackerel in the 1970s, and regulations restricting its harvest have considerably affected jack mackerel landings. From the mid-1920s through the early 1960s, the Pacific mackerel fishery was unregulated and was one of the most important commercial fisheries in California (Klingbeil 1983), but by the mid-1960s the fishery had collapsed. Virtually no Pacific mackerel were caught for the next ten years. Because of the reduced biomass, a moratorium on Pacific mackerel took effect in August 1970 (Klingbeil 1983). Regulations allowed up to 18% Pacific mackerel in loads of jack mackerel to minimize the negative impact a recovering Pacific mackerel population might have on the jack mackerel fishery. As the population started to recover in 1977, mixed catches with Pacific mackerel in excess of this limit occurred, interfering with the landing of jack mackerel (Klingbeil 1983).

When the 1977 spawning biomass of Pacific mackerel was assessed at 30,000 tons, the moratorium was lifted, and a quota system was implemented. When a season's quota was filled, "interseason" regulations took effect. These restricted the percentage of Pacific mackerel that could be landed with jack mackerel until fishing on the next Pacific mackerel quota began. The allowable percentage of Pacific mackerel changed several times over the next few years, ranging from 18% to 50%. In the 1977–79 seasons, daily or weekly landing limits were imposed on mixed mackerel catches with high percentages of Pacific mackerel to delay reaching the quota. This shifted the effort of the larger vessels toward jack mackerel as long as they were available in relatively pure schools. Pacific mackerel landings increased to the point of dominating combined mackerel landings by the 1979 season and continued to dominate them for the next four seasons (figure 1).

Details on the remarkable recovery of the Pacific mackerel and the regulations governing it have been covered by Klingbeil (1983). The overall effect of these regulations on jack mackerel landings is hard to assess. Although tolerance levels were intended to keep pressure off the Pacific mackerel population, the restrictions may have also limited jack mackerel landings during periods when jack mackerel could not be found schooling as a single species. Overall, the regulations probably slowed the redirection of fishing effort from jack to Pacific mackerel.

ECONOMIC CONSIDERATIONS

Jack mackerel are sold almost exclusively to canneries, and these canneries often limit the volume of landings they will accept (MacCall and Stauffer 1983). Canning capacities, stock on hand, and competition from other mackerel products, both foreign and domestic, have affected the volume of jack mackerel landed. Cannery orders limited landings in 1954, 1955 (Knaggs 1974a), 1959, 1960 (Knaggs 1974b), and 1977 (Mason 1989). Cannery capacity was reduced during the 1973–75 seasons after one cannery burned (Mason 1989). Cannery capacity in 1979 was estimated to be 80,000 MT (MacCall et al. 1980). Jack mackerel landings have not reached this level, partly because other species such as Pacific bonito (*Sarda chiliensis*) are also packed by these canneries, and partly because of the limited market for canned mackerel. Combined jack and Pacific mackerel landings since 1978 have only slightly exceeded the 45,000 MT of jack mackerel landed in 1977 (figure 1). Pacific mackerel are often found closer to shore than jack mackerel, decreasing fuel costs and making Pacific mackerel a more profitable target, as happened in the 1978 season (Mason 1989).

Purse seiners catch various species of pelagic fish. The selection of target species is one economic factor in which fishermen have some control. Profits are maximized by shifting effort among a variety of pelagic schooling fish as availability, marketability, and the opening and closing of fishing seasons and quotas allow. The fleet fished for sardines in the 1954 and 1955 seasons when availability increased and the price of jack mackerel was down, and in 1958 when sardines were again available and jack mackerel were unavailable. When other more profitable species such as Pacific bonito (in 1967, 1971) and both bonito and bluefin tuna, *Thunnus thynnus*, (in 1972, 1973, 1974, and 1980) became more available, fishermen shifted their effort for weeks or months to these species. In the fall of 1967, the fishing effort of the purse seine fleet was directed toward bonito, but price disputes over bonito and anchovy stopped all fishing by the fleet for three months (Fleming and Knaggs 1977). Thus the availability of different species to the purse seine fleet enhances fishermen's income, but confuses the interpretation of jack mackerel catch statistics as representative of availability.

There have been other causes for the fluctuations in catch during the history of the jack mackerel fishery (figure 2). Scarcity of fish was blamed for the reduced catches in 1953 (Knaggs 1974a), 1957, 1958 (Knaggs 1974b), 1966 (Knaggs and Barnett 1975), 1972–74, 1979, and 1983 seasons (Mason 1989).

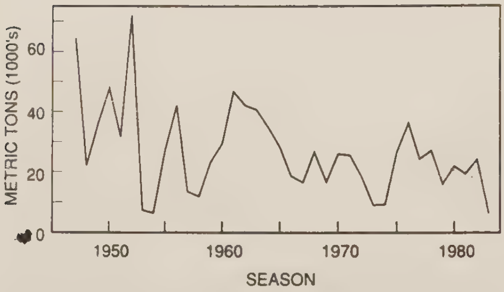

Figure 2. Landings of jack mackerel in southern California by season (1 August to 31 July).

These were many of the seasons with the lowest catches. Other factors had noticeable effects in certain seasons. In 1969, high levels of the pesticide DDT were found in jack mackerel, making it unfit for human consumption. Only pet food could be produced for six months until fish with lower DDT levels were caught (Fleming and Knaggs 1977). Several months of bad weather may have been one factor in reducing the jack mackerel catch in the 1972, 1973, and 1982 seasons (Mason 1989); however, weather conditions severe enough to prevent fishing lasted only a few months, so it was not rough weather alone that caused severe drops in seasonal landings. During the 1983 El Niño, however, jack mackerel were unavailable in southern California throughout the fall; the wetfish fleet moved north to Monterey, where most of the season's jack mackerel landings were made (Mason 1989).

In summary, the following factors have affected the jack mackerel landings by season:

- Landings of sardines: 1954, 1955, 1958
- Landings of anchovy: 1973, 1974, 1977, 1980
- Landings of Pacific mackerel: 1979–83
- Landings of bonito and/or bluefin tuna: 1967, 1971, 1973, 1974, 1977, 1980
- Market conditions: 1954, 1955, 1959, 1960, 1977
- Reduced cannery capacity: 1973–75
- Scarcity of schools of jack mackerel: 1953, 1957, 1958, 1966, 1972–74, 1979, 1983
- El Niño events: 1958, 1983
- DDT levels: 1969

POPULATION ASSESSMENT

Sampling Methods

The California Department of Fish and Game samples jack mackerel at the Terminal Island canneries. There is no closed season on jack mackerel fishing, so for reporting purposes, the season has been 1 August to 31 July of the following calendar year (Knaggs 1974a). The sampling plan has changed several times since 1947. Sampling methods for various periods are presented in a series of technical reports published by the California Department of Fish and Game (Knaggs 1974a,b; Knaggs and Barnett 1975; Fleming and Knaggs 1977; Mason 1989). The reports include estimates of numbers of fish landed for each month, and age composition.

Age Composition

The fish caught by the southern California purse seine fleet are less than 400 mm FL and under 8 years old. Fish larger than 400 mm FL are rarely caught by the purse seine fleet, but are taken incidentally by the salmon and albacore troll fisheries off California and Oregon, and by the offshore whiting trawl fishery (MacCall et al. 1980). Some of these larger fish have been over 30 years old (Fitch 1956). Thus the purse seine fishery harvests jack mackerel from a limited segment of the total population.

The age composition of the jack mackerel landings has not been consistent throughout the history of the fishery. The average age of the fish caught by the wetfish fleet has decreased markedly. In the first decade of the jack mackerel fishery (1947–56) the catch was dominated by fish age 3 or older (figure 3). Younger fish contributed no more than 16,000 MT (35 million pounds) to the fishery per season. The next eight seasons (1957–64) appear to be a transition period when the weight of younger fish reached a level of about 18,000 MT (40 million pounds) per season, but older fish still contributed significantly to the catch in some years. In the final period (1965–83) fish younger than age 3 continued

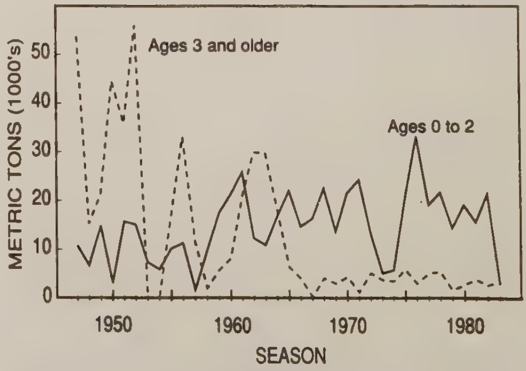

Figure 3. Jack mackerel landings divided into two age groupings: 0–2 (*solid line*) and 3 and older (*dashed line*).

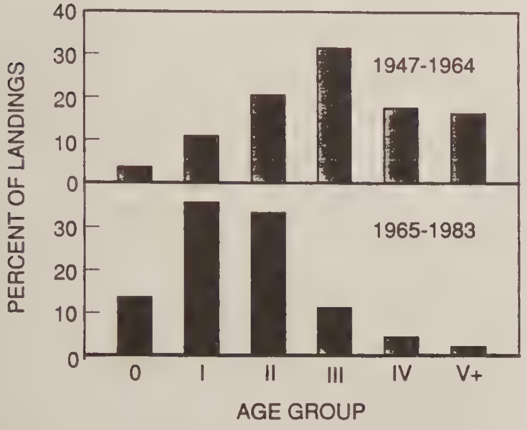

Figure 4. Age composition of jack mackerel landings from two time periods.

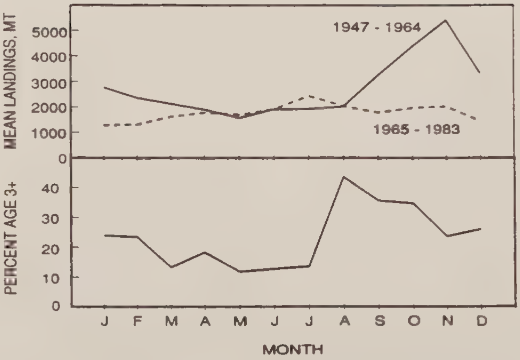

Figure 5. Seasonality of jack mackerel in southern California. *Upper panel*, mean seasonal landings from 1947 to 1964 (*solid line*) and 1965 to 1983 (*dashed line*). *Lower panel*, landings of fish age 3 and older from 1972 to 1983 as a percentage of each month's landings.

to be caught at about the 18,000-MT (40-million-pound) level, consistently dominating the catch, while older fish dropped out of the fishery, contributing less than 7,000 MT (15 million pounds) per season. Thus the catch shifted from older to younger fish during the middle 1960s.

A comparison of the age composition of the 1947–64 period with the 1965–83 period (figure 4) reveals that the earlier period was dominated by age-3 fish, whereas the later period was dominated primarily by age-1 fish and secondarily by age-2 fish. During the earlier period, fish of age 3 or older composed 65% of the catch; in later years those age groups contributed only 18%.

Seasonality in Age Composition

During the early period (1947–64), when older fish appeared in the fishery, the highest landings were made during the late fall, and the lowest landings during spring and summer (figure 5). This pattern reflected increased fishing effort at the opening of the sardine season (October 1) from boats looking primarily for sardines, but prepared to catch Pacific mackerel or jack mackerel if they could not find sardines (Roedel 1952). The lower catches of jack mackerel in the spring of these earliest years were associated with decreased fishing effort in the late spring when the sardine season was closed and Pacific mackerel was seasonally unavailable (Roedel 1953). However, by 1950 the fleet discovered that jack mackerel did not always disappear in the spring, and fishing continued year-round. More recently, from 1965 to 1983, seasonality was reduced, with only a slight peak in July. During this period, anchovy was the alternate fishery available to the purse seine fleet, and the closure of the anchovy reduction season, in May or June, increased fishing pressure on jack mackerel during the summer.

A seasonal pattern also appears in the age composition of the catch. Landings from 1972 to 1983 were examined on a monthly basis for age composition (data for earlier years were unavailable). Even during this period, when older fish were less commonly caught, fish age 3 and older composed more than one-third of the catch from August through October (figure 5). They contributed less than 25% of the catch during the rest of the season, and less than 15% during May, June, and July.

The age composition of the catch was undoubtedly influenced by the interaction of two seasonal factors: (1) larger fish were most often caught in the fall, and (2) the fall fishery contributed less after 1964. Using the monthly age composition data from the later period (1972–83) on mean monthly landings from the earlier period (1947–64) to estimate the contribution of fish of age 3 and older in the earlier period gives an expected 25% of the season's catch as age 3 or older. However, age 3 and older fish actually composed 65%, not 25%, of the catch in the earlier period. Therefore changes in the seasonality of fishing effort explain only a small proportion of the change in age composition.

Recruitment

The relative strength of different year classes has varied widely throughout the history of the jack mackerel fishery. To minimize confusion with variations in seasonal cannery production, comparisons of different year classes are based on the relative virtual year-class strength as described by MacCall and Stauffer (1983). These strengths are produced by summing the percentage contribution of a year class (from numbers of fish) to each season it appeared in the fishery. For example, the 1970 year class contributed 30% of the season's catch as young-of-the-year in 1970, 65% of the 1971 catch as 1-year-olds, 37% as 2-year-olds, 17% as 3-year-olds, 14% as 4-year-olds, and 3% as 5-year-olds, for a total index of 165. An average year class would contribute about 100%, and an above average class would contribute more by providing a higher percentage of the catch than surrounding year classes. Year classes are effectively compared only with other year classes occurring simultaneously in the fishery.

The series of year classes can broken into three periods with different patterns of strength. During the first period, from the first fully represented year class in 1947 until 1958, strongly represented jack mackerel year classes in 1947, 1952, 1953, and 1958 (figure 6) were separated by strings of weakly represented year classes. The second period (1959–73) had clusters of strongly and weakly represented year classes, with the dominant 1958 year class being followed by two strong ones in 1959 and 1960. The next four year classes (1961–65) contributed much less to the catch, and stronger classes followed from 1966 to 1970 (especially 1967 and 1970), with less-dominant year classes in 1971–73 (figure 6). The third period (1974–80) features a remarkable series of alternating strong and weak year classes. The 1974, 1976, 1978, and 1980 classes were all relatively strong, whereas those of 1973, 1975, 1977, and 1979 were relatively weak. A scarcity of young fish in southern California during the 1982–83 El Niño enhanced the relatively high year-class strength of 1980.

Variability in year-class strength is an important factor in the age composition of the catch. In the early period of the fishery (1947–58) relatively strong year classes were separated by strings of four much weaker classes. Fish from the more prominent year classes dominated the catch until another strong class appeared five years later. Only a strong year class could contribute large numbers of fish for several seasons. As the relatively strong 1958, 1959, and 1960 year classes disappeared from the fishery (in 1964), and there were not any strong year classes to provide large numbers of older fish, the catch became limited to ages 0 to 3. After the 1966 season, relatively strong year classes appeared frequently, usually every two to three years, so younger fish were readily available. If younger fish were easier to catch, they might have been expected to dominate the catch as long as there was a ready supply of them.

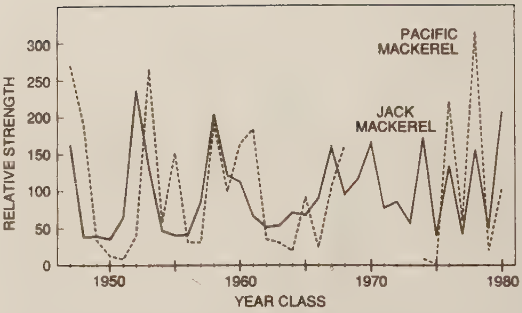

Figure 6. Recruitment strength of year classes of jack mackerel (*solid line*), and Pacific mackerel (*dashed line*), as measured by the sum of the percentage contribution of each year class to seasonal landings in southern California.

However, if older fish were still present, one would expect to have seen older fish during the 1973 and 1974 seasons, when young jack mackerel were hard to find. The catch during this period, although reduced, remained ages 0 to 2. The relatively strong 1970 year class did not appear strongly in the catch after age 2 (Mason 1989, table 18). To some extent, the frequency of relatively strong year classes may have contributed to the shift toward younger fish in the fishery.

DISCUSSION

Decline in Age Composition

The decline in the abundance of older fish in the catch stands out as an important change in the fishery. What has produced this change? Two factors presented above have contributed to this decline. First, the distribution of fishing effort during the season combined with the pattern of large fish being available in the fall accounts for part of the change in age composition. Second, the higher frequency of relatively strong year classes since 1965 may explain some of the decline in abundance of older fish.

But these factors don't appear to account for all of the change observed. Overfishing should be examined to see if it contributed to the change. Economic factors have both enhanced and reduced fishing pressure at different times, affecting the ages at which particular year classes were caught. Shifts in effort from one species to another may have added complications in fishing techniques and spatial distribution. Environmental factors may have affected different ages in different ways. By examining these factors we may be able to tell which ones have contributed to the change in the age composition of the catch.

The decreased abundance of older fish in the catch between the early years of the fishery and the post-1965 period could reflect a true reduction of older fish in the population, or only a decline in their contribution to the southern California fishery. It is not possible to assess changes in the age composition of the whole population, since only young jack mackerel are harvested, and the fishery operates over a small portion of the total range. Although it is likely that some of the change in the age composition in the very earliest years (1947–51) is attributable to the presence of older fish from year classes unexploited before the fishery began, these fish disappeared from the landings by 1953 (Knaggs 1974a, table 17). They do not account for older fish present from 1954 to 1964. MacCall and Stauffer (1983) estimated that fish age 8 or younger compose less than two-thirds of the population, and that the purse seine fleet harvests only a small percentage (13%–20%) of the potential yield of this age group. If this is true, then the decline in older fish in the catch reflects a change in what is caught by the fishery, not a decline in the population due to overfishing.

Depressed market conditions were an economic factor that affected the age at which jack mackerel were caught in some seasons. During the 1953 and 1954 seasons the low price of imported mackerel protected the 1952 year class from exploitation as 1- and 2-year-olds (Knaggs 1974a), so more fish from this year class were caught at older ages in 1955–57. However, the 1958–60 year classes did not have this protection as young fish (except in the 1958 season, when sardines were being caught) but still contributed large amounts to the catch as 3- and 4-year-olds. Thus depressed market conditions had a limited effect on age composition.

Although it is possible that some undocumented changes in fishing tactics caused by the shift in fishing effort from sardines to anchovy may have contributed to the decline in age composition, I could find no evidence to support this theory. It appears that the change in age composition truly reflects the age of fish available to the purse seine fleet.

Another factor that may have contributed to the change in apparent age composition is related to the areas fished. Before 1965, sardines were the most desirable species to the purse seine fleet, followed by Pacific mackerel; therefore, boats fished where they expected to find sardines or Pacific mackerel. Most of the jack mackerel landed before 1965 came from the Channel Islands area off Santa Barbara or the area near San Pedro harbor (Clothier and Greenwood 1956; Duffy 1968). Boats rarely fished the more southern areas around San Clemente Island and Tanner and Cortez banks. However, from 1964 to 1971, when sardines and Pacific mackerel were absent, most of the catches were from these offshore southern areas (MacCall et al. 1980). This leads to the assumption that more fish from older age groups are caught in the Channel Islands area or the area near San Pedro harbor than on Tanner and Cortez banks. This assumption cannot be rigorously examined because information about catch locations is inadequate. The assumption does not hold true for the 1952 season, when older fish composed 79% of the catch, and 78% of the catch came from San Clemente Island and Tanner and Cortez banks (Knaggs 1974a, tables 2 and 15). In addition, since the return of Pacific mackerel in 1977, the fleet has spent more of its effort inshore, in search of Pacific mackerel (Anon. 1980), but the large jack mackerel once caught inshore have not reappeared in the catch.

The fact that small jack mackerel are found in shallow schools fishable by southern California purse seiners, and that fish larger than 400 mm FL are found in other areas, either offshore or farther north (MacCall et al. 1980), suggests that the fish may have altered their behavior since 1965. Increases in sea-surface temperature or changes in ocean circulation patterns in southern California could have caused some jack mackerel to move to more northern, or deeper cool waters at an earlier age.

It seems that the change in the age composition of the jack mackerel landings between the 1947–64 period and the post-1964 period cannot be ascribed to just one cause, but is probably due to several factors: (1) changes in the seasonal pattern of the fishery, (2) the frequency of relatively strongly recruited year classes, (3) economic factors, (4) shifts in the areas fished, and (5) changes in fish behavior.

Recruitment Variability

Both jack mackerel and Pacific mackerel have shown a high degree of recruitment variability from year to year. Because both species are taken by the same fleet and are of similar ecological type, it is very likely that environmental conditions might have correlated effects on recruitment. To compare the recruitment success of the two species, relative virtual population estimates were developed for Pacific mackerel. Catch by age and season, from table 6 of Parrish and MacCall (1978), was used to calculate relative year-class strengths in Pacific mackerel from 1947 to 1967. Similar data from table 3 of MacCall et al. (1985) were used to calculate relative year-class strength for 1974 to 1980. There is a gap in the time series from 1969 to 1973 because there was no fishery for Pacific mackerel (and therefore no data) for the years when the fishery had collapsed. A correlation significant at the $p < 0.05$ level exists between the reproductively successful year classes for Pacific mackerel and successful year classes of jack mackerel ($r = .385$, df = 29). A comparison of jack and Pacific mackerel (figure 6) shows that both species had relatively successful year classes in 1947, 1953, 1958–60, 1967, 1976, 1978, and 1980. The 1974 year classes were also relatively successful for both species; however, the Pacific mackerel success is not apparent from figure 6, because it was this year class that started the recovery of the Pacific mackerel population (Anon. 1979), and its relative strength is underestimated because the moratorium was not lifted until 1977.

It is also interesting to note that these successfully recruited year classes for both Pacific and jack mackerel are opposite to (and alternating with) successfully recruited year classes for combined rockfish species (*Sebastes dalli* and *S. saxicola*) taken as juveniles in quarterly trawl surveys in southern California. Mearns et al. (1980) indicated that the peak catch years for juveniles of these species were 1971, 1973, 1975, and 1977—all very poor years for mackerel recruitment (figure 6). These years for the Santa Monica Bay and Orange County coastline had cool or cooling water with decreasing clarity. Thus conditions favorable for demersal rockfish recruitment may be very different from those supporting good pelagic mackerel recruitment.

CONCLUSIONS

The high variability in landings seen in the southern California jack mackerel catch is due in some years to a lowered availability of jack mackerel and in other years to interspecific interactions within the wetfish fishery, as well as to economic factors. The decline in abundance of older fish in the catch after 1964 is partially caused by a decline in fall fishing effort. The increased frequency of relatively strong year classes after 1964 increased the availability of young fish. Changes in the areas fished by the wetfish fleet may have also contributed to catching younger fish. Nevertheless, the disappearance of older fish cannot be explained solely by fishery interactions, and may reflect a real change in the availability of these age groups to the purse seine fishermen. Pacific mackerel recruitment has also varied, and in most cases jack and Pacific mackerel have shown similar patterns in relative year-class strength.

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LITERATURE CITED

Anon. 1979. Review of the pelagic wet fisheries for 1976 with notes on the history of these fisheries. Calif. Coop. Oceanic Fish. Invest. Rep. 20:6–9.

———. 1980. Review of the pelagic wet fisheries for 1978 and 1979. Calif. Coop. Oceanic Fish. Invest. Rep. 21:8–11.

———. 1984. Review of some California fisheries for 1983. Calif. Coop. Oceanic Fish. Invest. Rep. 25:7–15.

Clothier, C. R., and E. C. Greenwood. 1956. Jack mackerel and sardine yield per area from California waters, 1946–47 through 1954–55. Calif. Dep. Fish Game Fish Bull. 102:7–16.

Duffy, J. M. 1968. Jack mackerel yield per area from California waters 1955–56 through 1963–64. Calif. Fish Game 54:195–202.

Fitch, J. E. 1952. The decline of the Pacific mackerel fishery. Calif. Fish Game 38:381–389.

———. 1956. Jack mackerel. Calif. Coop. Oceanic Fish. Invest. Prog. Rep. 1955–56:27–28.

Fleming, E. R., and E. H. Knaggs. 1977. The southern California jack mackerel fishery and age, length and sex composition of the catch for the 1967–68 through 1971–72 seasons. Calif. Dep. Fish Game, Mar. Res. Tech. Rep. 37:1–44.

Klingbeil, R. A. 1983. Pacific mackerel: a resurgent resource and fishery of the California Current. Calif. Coop. Oceanic Fish. Invest. Rep. 24:35–45.

Knaggs, E. H. 1974a. The southern California jack mackerel fishery and age composition of the catch for the 1947–48 through 1956–57 seasons. Calif. Dep. Fish Game, Mar. Res. Tech. Rep. 22:1–47.

———. 1974b. The southern California jack mackerel fishery and age composition of the catch for the 1957–58 through 1961–62 seasons. Calif. Dep. Fish Game, Mar. Res. Tech. Rep. 24:1–25.

Knaggs, E. H., and P. A. Barnett. 1975. The southern California jack mackerel fishery and age composition of the catch for the 1962–63 through 1966–67 seasons. Calif. Dep. Fish Game, Mar. Res. Tech. Rep. 28:1–28.

Knaggs, E. H., and J. S. Sunada. 1974. Validity of otolith age determinations for jack mackerel, *Trachurus symmetricus*, from the Southern California Bight area. Calif. Dep. Fish Game, Mar. Res. Tech. Rep. 21:1–11.

MacCall, A. D., and G. D. Stauffer. 1983. Biology and fishery potential of jack mackerel (*Trachurus symmetricus*). Calif. Coop. Oceanic Fish. Invest. Rep. 24:46–56.

MacCall, A. D., H. W. Frey, D. D. Huppert, E. H. Knaggs, J. A. McMillan, and G. D. Stauffer. 1980. Biology and economics of the fishery for jack mackerel in the northeastern Pacific. NOAA Tech. Memo. NMFS-SWFC-4.

MacCall, A. D., R. Klingbeil, and R. D. Methot. 1985. Recent increased abundance and potential productivity of Pacific mackerel (*Scomber japonicus*). Calif. Coop. Oceanic Fish. Invest. Rep. 26:119–129.

Mason, J. E. 1989. The southern California jack mackerel fishery, and the age and length composition of the catch for the 1972–73 through 1983–84 seasons. Calif. Dep. Fish Game, Mar. Res. Tech. Rep. 58: 1–39.

Mearns, A. J., M. J. Allen, M. D. Moore, and M. J. Sherwood. 1980. Distribution, abundance and recruitment of soft-bottom rockfishes (Scorpaenidae: Sebastes) on the southern California mainland shelf. Calif. Coop. Oceanic Fish. Invest. Rep. 26:180–190.

Parrish, R. H., and A. D. MacCall. 1978. Climatic variation and exploitation in the Pacific mackerel fishery. Calif. Dep. Fish Game, Fish Bull. 167:1–110.

Roedel, P. M. 1952. A review of the Pacific mackerel (*Pneumatophorus diego*) fishery of the Los Angeles region with special reference to the years 1939–1951. Calif. Fish Game 38:253–273.

———. 1953. The jack mackerel, *Trachurus symmetricus*: a review of the California fishery and of current biological knowledge. Calif. Fish Game 39:45–68.

Wine, V. L., and E. H. Knaggs. 1975. Maturation and growth of jack mackerel, *Trachurus symmetricus*. Calif. Dep. Fish Game, Mar. Res. Tech. Rep. 32:1–26.

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Ecology of pelagic larvae and juveniles of the genus *Sebastes*

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Synopsis

Pelagic larvae and juveniles of the genus *Sebastes* are widely distributed in the continental shelf and slope waters of subarctic to temperate oceans, with greatest abundance in the Northern Hemisphere. We review the ecology and distribution of these planktonic and micronektonic life stages in relation to oceanographic conditions. Special attention is paid to the west coast of North America, where abundance of larvae from samples collected during 1951–1981 is described. After transformation, the pelagic juveniles are widely distributed, often at great distances from benthic adult habitats. These stages are most frequently distributed in either midwater or near-surface habitats; this dichotomy may require different strategies for successful recruitment.

Introduction

After parturition, larvae of the genus *Sebastes* lead a pelagic existence of varying duration and are one of the most abundant kinds of fish larvae in the temperate and subarctic North Atlantic and North Pacific Oceans (Ahlstrom 1961, Bainbridge & Cooper 1971). Relatively little is known about their ecology or that of the older micronektonic juveniles. One of the major stumbling blocks to research on these age groups is the difficulty in identifying them to species (Moser et al. 1977). Published studies, however, reveal interspecific variation in parturition seasons, vertical and horizontal distributions of larvae, habitats occupied between the larval period and settlement and duration of the planktonic phase. In this paper, we review the literature on the pelagic, early life history stages of *Sebastes* and describe the distribution and ecology of larvae in the California Current region.

Spawning periodicity

The timing of spawning is critical to the survival of fish larvae. In *Sebastes*, insemination may precede fertilization by 6 months (Sorokin 1961), and parturition is equivalent to spawning in oviparous fishes. Timing of spawning in marine fishes is often related to feeding seasonality of adults, allowing needed energy reserves (Guillemot et al. 1985). Alternatively, features in the pelagic environment where the larvae reside, particularly physical factors and prey concentrations, may be of critical importance (Iles & Sinclair 1982). Parrish et al. (1981) suggested that fish species off the west coast of North

America have evolved to spawn in winter when upwelling and the attendant offshore Ekman transport are minimal. Their hypothesis is only partially supported by an examination of the spawning seasonality of *Sebastes* species off this coast (Wyllie Echeverria 1987); many species also spawn in summer months, and the extended larval periods may subject their larvae to offshore dispersal. Further, certain species may spawn more than a single brood (Moser 1967, MacGregor 1970). Within species, spawning seasonality may be distinct with a clear peak (Anderson 1984) or extended with a minor peak. For example, the year-round presence of small, pelagic, juvenile *S. diploproa* suggests that at least limited spawning occurs in all months of the year (Boehlert 1977).

Distribution patterns of larvae

Atlantic

In the North Atlantic, ichthyoplankton surveys reveal that larvae of *Sebastes* are seasonally abundant and widespread; Tåning (1949) showed that larval *Sebastes* were abundant in the Atlantic north of 50° latitude where boreal mixed water of 3–8.5° C was at depths of 200–500 m (see also Templeman 1959). Subsequent surveys in the Norwegian and Barents seas (Baranenkova & Khokhlina 1961), central Atlantic (Einarsson 1961, Henderson 1961, Bainbridge & Cooper 1971) and western Atlantic (Templeman 1959) generally confirmed Tåning's (1949) observations, and the central Atlantic surveys revealed a vast concentration of *Sebastes* larvae in the Irminger Sea southwest of Iceland. Because of the difficulty in distinguishing the larvae of *S. marinus*, *S. mentella* and *S. fasciatus*, some conclusions of these studies apply to the genus as a composite, and definitive information on individual North Atlantic species awaits improvement in the taxonomy of larvae (Kendall 1991).

Southern oceans

The genus may be represented by only a single species, *S. capensis,* in the Southern Hemisphere, present in both Atlantic and Pacific oceans (Chen 1971). Very little information is available on distributions of larvae of this species, partly due to its relative scarcity in plankton collections. For example, *S. capensis* represented only 0.05% of all larvae collected off northern Chile (Loeb & Rojas 1988). Sanchez & Acha (1988) reported catches of *S. oculatus (S. capensis?)* larvae and pelagic juveniles over the Patagonian shelf between 39° and 55° latitude. Although overall occurrences were low (5.5% of positive tows), abundance (number per 10 m^2) reached a peak of 55% of the total catch of larvae in December. This suggests that populations of *Sebastes* off Chile and Argentina may be fundamentally different. More research will be necessary to describe the species composition, distribution and abundance of *Sebastes* larvae in the Southern Hemisphere.

North Pacific

Wide-ranging ichthyoplankton surveys have not been made in the western Pacific. A number of localized surveys showed that larvae of several *Sebastes* species are seasonally abundant and generally confined to the coastal shelf: *S. inermis* (Harada 1962, Okiyama 1965, Kim et al. 1985), *S. pachycephalus* and *S. hubbsi* (Senta 1962), *S. pachycephalus, S. oblongus* and *S. marmoratus* (Kuwahara & Suzuki 1983).

Numerous ichthyoplankton surveys have been conducted in the Bering Sea and Gulf of Alaska. Waldron (1981) summarized ichthyoplankton data available for the former and found that larvae of *Sebastes* occurred in spring and summer samples from two regions. Most larvae occurred from the Aleutian Islands north to about 60° N over the continental slope and adjoining regions. A second area of concentration was near Bowers Ridge in the southwestern Bering Sea. Lisovenko (1967) described the distribution and abundance of *S. alutus* larvae from an ichthyoplankton survey in the Gulf of Alaska. His description of diagnostic taxonomic features of the larvae, however, is not convincing, and his conclusions probably apply to a mixture of species. He reported much higher densities of *Sebastes* larvae in the northern region of the Gulf of Alaska than in areas to the west and east and postulated that larvae were entrained in the anticyclonic gyre of the Alaska Current. This was not corroborated by LeBrasseur's (1970) surveys, which covered much of the Gulf of Alaska. *Sebastes* had the highest incidence of all types of larvae; they were concentrated over the continental shelf and slope west of the Queen Charlotte Islands, with some encountered seaward to 300 nmi.

Kendall & Dunn (1985) presented data on the distribution of *Sebastes* larvae from 11 ichthyoplankton surveys conducted over the continental shelf off Kodiak Island, Alaska. Larvae first appeared along the edge of the shelf in spring, were abundant and widely distributed over the shelf in summer and were generally restricted to midshelf in fall cruises. The authors suggested that this apparent shift in distribution resulted from differential timing of extrusion among species. Kendall & Ferraro (1988) also found high densities of *Sebastes* larvae along the continental slope in a more wide-ranging survey between the Kenai Peninsula and Umnak Island, March-June 1985. As in Kendall & Dunn (1985), their sampling pattern was restricted to the slope region and did not demonstrate the full seaward extent of *Sebastes*. A comprehensive view of the areal and temporal distribution of *Sebastes* larvae in the Gulf of Alaska and Bering Sea in relation to major oceanographic features will require annual, wide-ranging surveys.

Sebastes spp. was the most abundant taxon of fish larvae taken on a survey during April-May 1967 from Vancouver Island, Canada, to the Oregon-California border, accounting for 29% of the total fish larvae (Waldron 1972). Larvae were concentrated over the continental shelf and slope, but were found seaward to > 250 nmi and were unusually abundant near Cobb Seamount. Larvae of *Sebastes* occurred prominently in several surveys along the Oregon coast (Richardson & Pearcy 1977, Richardson et al. 1980). Highest mean abundances occurred over the outer continental shelf, or beyond it, where *Sebastes* spp. were dominant components of the offshore ichthyoplankton assemblage. Richardson et al. (1980) proposed that longshore coastal currents help maintain the distinct inshore and offshore assemblages and that a cellular circulation pattern near the continental slope works in concert with seasonal onshore-offshore surface drift to transport *Sebastes* larvae seaward in summer and shoreward in winter.

In a series of ichthyoplankton surveys off the Washington, Oregon and northern California coasts, larvae of *Sebastes* spp. were abundant and widespread both latitudinally and offshore during spring months (Kendall & Clark 1982). Larvae became more restricted to coastal waters in summer and latitudinally patchy along the coast during fall and early winter. Larvae from oblique bongo net samples were consistently smaller (peak length frequency at 3–5 mm) than those caught in neuston (surface) tows (modal peak in the 10–30 mm range). This is consistent with the relatively high densities of rockfish larvae and juveniles captured by Shenker (1988) in a large neuston trawl. These data suggest that larvae of some *Sebastes* species utilize the surface waters as a prerecruitment habitat.

California Cooperative Oceanic Fisheries Investigations

Since 1939 the California Cooperative Oceanic Fisheries Investigations (CalCOFI) has carried out joint biological and oceanographic surveys off the west coast of the United States and Mexico, primarily off California and Baja California (Hewitt 1988). These surveys have produced the most extensive ichthyoplankton time series available, both temporally and spatially. The distribution and abundance of *Sebastes* spp. larvae have been described for segments of the time series (Ahlstrom 1961, Ahlstrom et al. 1978), and some progress has been made on the identification of individual species. Complete life history series of eight species have been established, and five of these (*S. aurora, S. jordani, S. levis, S. macdonaldi, S. paucispinis*) are sufficiently distinct to warrant their identification in recent CalCOFI survey samples (Moser et al. 1977, 1985). Complete early life history series of *S. melanostomus* (Moser & Ahlstrom 1978) and *S.*

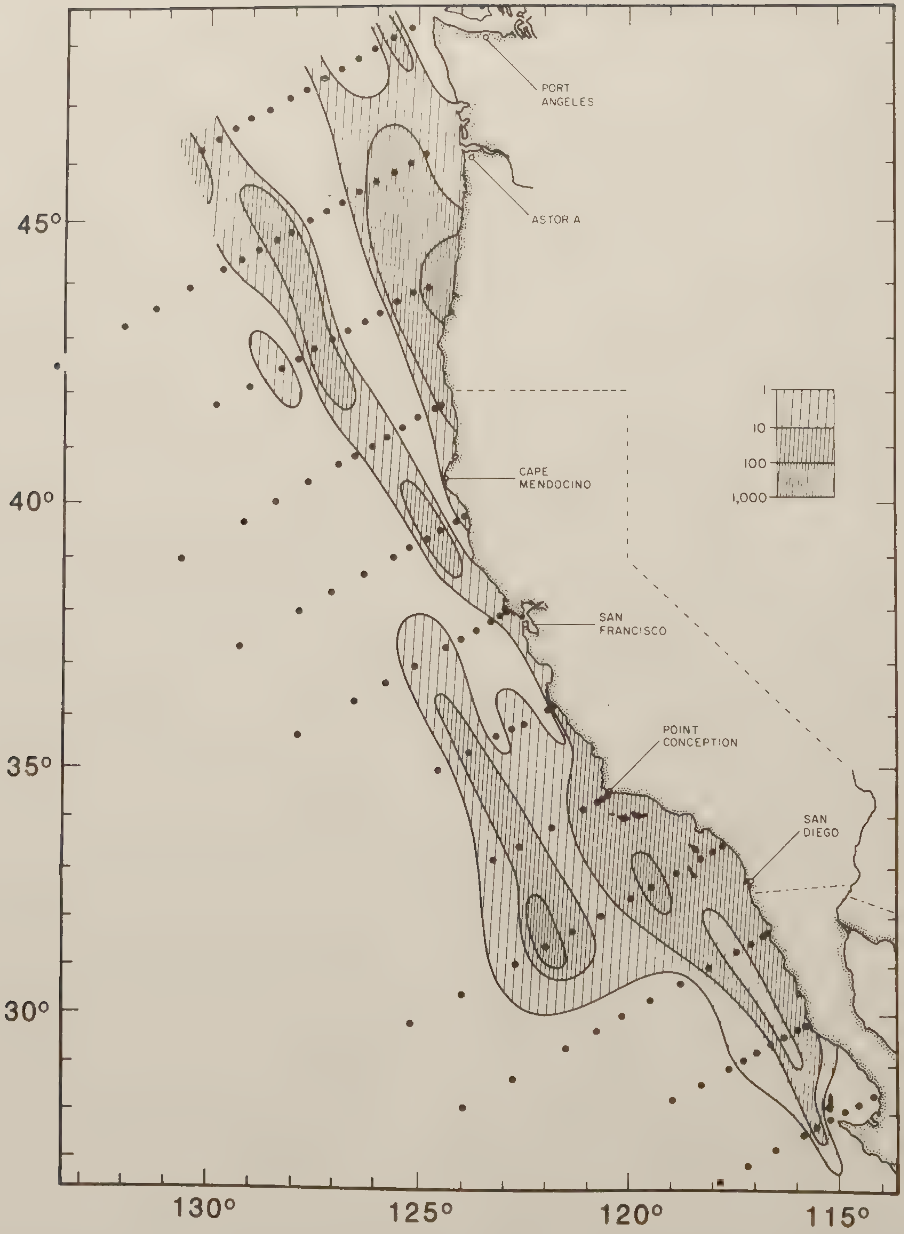
PORT ANGELES
ASTORIA
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
1
10
100
1,000
45°
40°
35°
30°
130°
125°
120°
115°

Fig. 1. Relative abundance of *Sebastes* spp. larvae (number under 10 m^2) taken off Washington, Oregon, California and Baja California during CalCOFI cruise 7205 (modified from Ahlstrom et al. 1978).

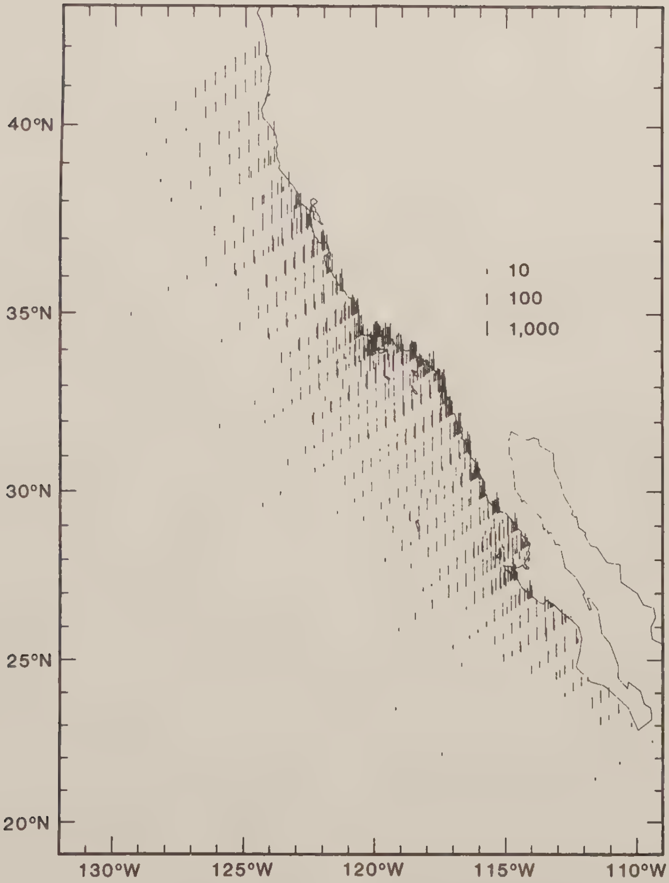

Fig. 2. Summed abundance (number under 10 m²) of *Sebastes* spp. larvae collected on CalCOFI surveys during 1951–1981; numbers indicated by exponentially scaled bars.

dallii (Moser & Butler 1981) have been described, but their larvae have not been routinely identified in CalCOFI samples because of the possibility of confusion with closely related species. Larvae of *S. cortezi* were identified only in CalCOFI samples taken in the Gulf of California during 1957 and 1958. In this paper, we utilize the recently established CalCOFI ichthyoplankton data base (Ambrose et al. 1987) to describe the distribution and abundance patterns of *Sebastes* spp. from 1951 to 1981.

Off California and Baja California, as reported for other regions, *Sebastes* larvae are concentrated over the continental shelf and slope and are found as far as 300 nmi beyond the shelf (Fig. 1, 2). Distributions of larvae are patchy along the coast and certain regions (e.g. Cape Mendocino, San Francisco, Pt. Conception, Southern California Bight, and Pt. Eugenia) consistently have higher concentrations of larvae (for additional examples, see distribution maps in Ahlstrom et al. 1978). *Sebastes* larvae ranked fourth overall in abundance in the 1951–1981 CalCOFI time series, comprising 6.2% of all larvae collected (Smith & Moser 1988). Mean incidence (65%) and abundance (71 larvae per 10 m²) were highest off central California, were slightly lower off northern California and declined gradually toward the southern end of the survey

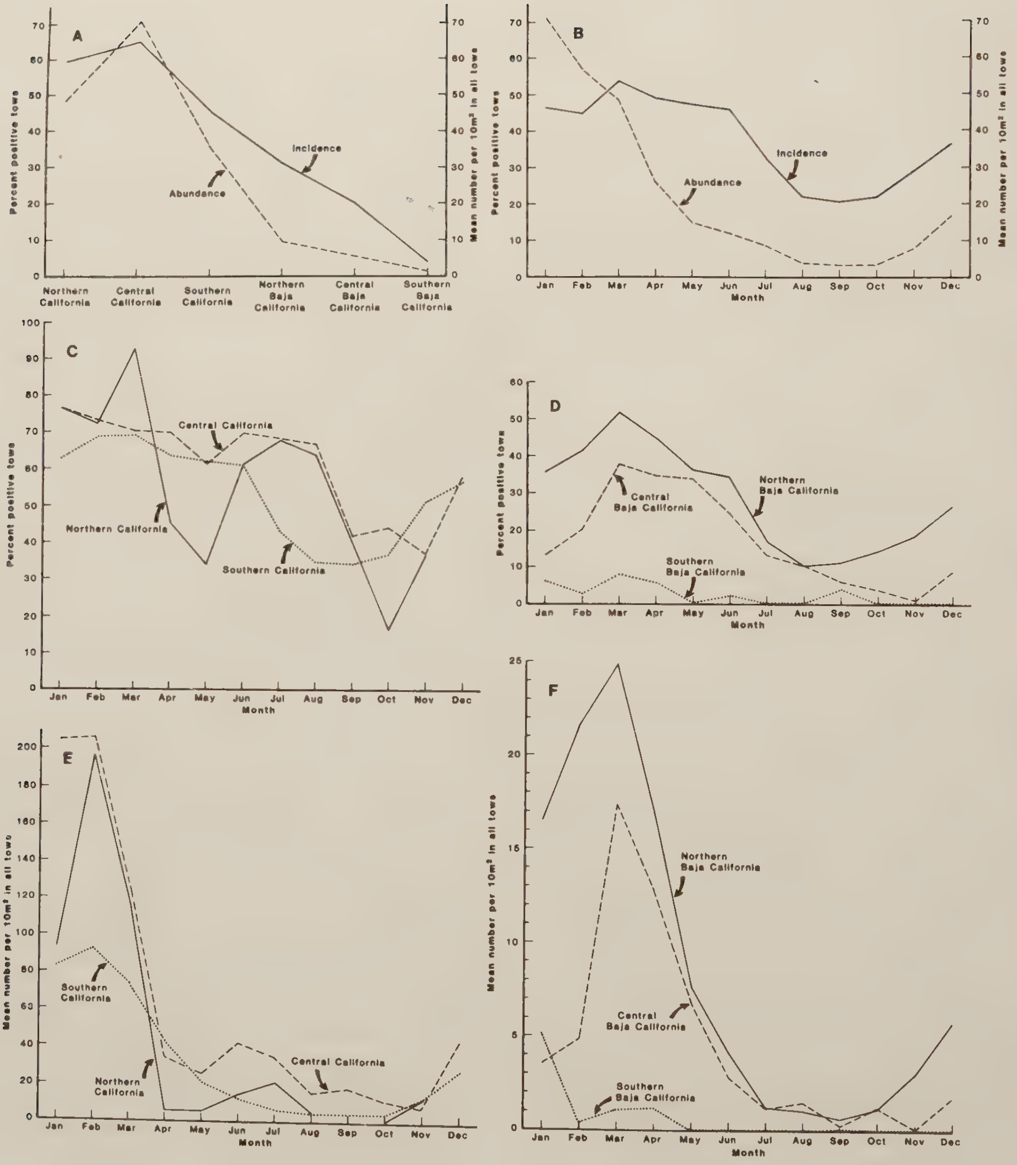

Fig. 3. Mean incidence (percent positive tows) and abundance (number under 10 m²) of *Sebastes* spp. larvae sampled on CalCOFI surveys off California and Baja California during 1951–1981. (A) overall incidence and abundance in six coastal zones; (B) seasonal incidence and abundance for entire CalCOFI survey area; (C) seasonal incidence for California; (D) seasonal incidence for Baja California; (E) seasonal abundance for California; (F) seasonal abundance for Baja California.

pattern (Fig. 3A). For all regions combined, mean incidence was high (>40%) from January through June with a peak of 54% in March (Fig. 3B). A July-September decline was followed by a gradual increase in October-December. Overall mean abundance was highest in January (71 larvae per 10 m^2), declined to one-tenth that value in August-September and then increased in October-December. The seasonal incidence of larvae captured off southern California was similar to that for all regions combined, but incidence off northern California was distinctly bimodal with peaks in March and June-August (Fig. 3C). Incidence for central California was intermediate between these two patterns. The north to south trend in seasonal incidence continued through Baja California (Fig. 3D). In the northern portion, a broad dome of relatively high incidence existed from January to June, followed by a gradual summer decline. Onset of peak incidence was later off central Baja California, and several small incidence peaks characterized southern Baja California.

Seasonal abundance was bimodal for northern and central California (Fig. 3E), but the summer peaks were much less pronounced than the corresponding peaks in incidence (Fig. 3C). The summer peak could be caused by either the release of a second brood of larvae by the same species that produced the January-March peak or release from a different group of species with a later parturition season. Alternatively, the summer peak could represent larvae that were produced north of the sampling area by summer-spawning species and then transported to northern and central California waters by the California Current. The summer peak was not evident in southern California (Fig. 3E). Abundance curves for Baja California clearly indicate a later onset of parturition and a broader spring peak compared with California, even though absolute values were one-tenth the former (Fig. 3F).

Regional maps of incidence and abundance of *Sebastes* larvae show seasonal onshore-offshore as well as latitudinal trends (Fig. 4). The late winter-early spring maxima for all coastal regions are clearly shown, with a sharp reduction off Baja California. The extent of offshore distribution of larvae is much greater off California than Baja California, where it is progressively more coastal towards the southern region of the peninsula. The seasonal bimodality off northern California appears in July-September as a gradient with highest values in the coastal zone. Because *Sebastes* spp. larvae are not abundant north of California in these months (Richardson & Pearcy 1977, Kendall & Clark 1982), they probably represent a late reproductive peak of northern California species. The offshore distribution of larvae is greatest off central California and is sustained throughout the year. Relatively high incidence and abundance are maintained along the coast through spring and summer. Off southern California, coastal incidence and abundance decrease after the January-March peak but increase in October-December, in advance of other coastal regions. The broad winter-spring peak in incidence and abundance off Baja California is evident in the regional maps, with offshore extent and relative values decreasing to the south.

Peak production of *Sebastes* larvae off California and Baja California coincides with low ocean temperatures in those regions and declines as seasonal warming progresses northward (Fig. 4; Reid et al. 1958). Mean zooplankton abundance is inversely related to temperature and is generally higher in coastal regions because of upwelling. Our data (not illustrated) indicate a close areal and seasonal match between zooplankton concentration and abundance of *Sebastes* larvae; peak abundance of larvae slightly precedes peak zooplankton abundance. The zooplankters retained by CalCOFI nets are generally larger than those eaten by fish larvae, however, and peak abundance of smaller copepods at younger stages may coincide more closely with abundance of *Sebastes* larvae.

Abundance of *Sebastes* larvae is characterized by large interannual variation off California and Baja California (Fig. 5A, B). Values for central and southern California were comparatively low during the 1950's, with a minimum in 1959 when a major period of ocean warming (El Niño) had reached its full effect. This was followed by a general trend of increasing abundance in the 1960's and 1970's, with peaks in 1963 and 1969 in central California and a peak in 1972 in southern California. Mean abun-

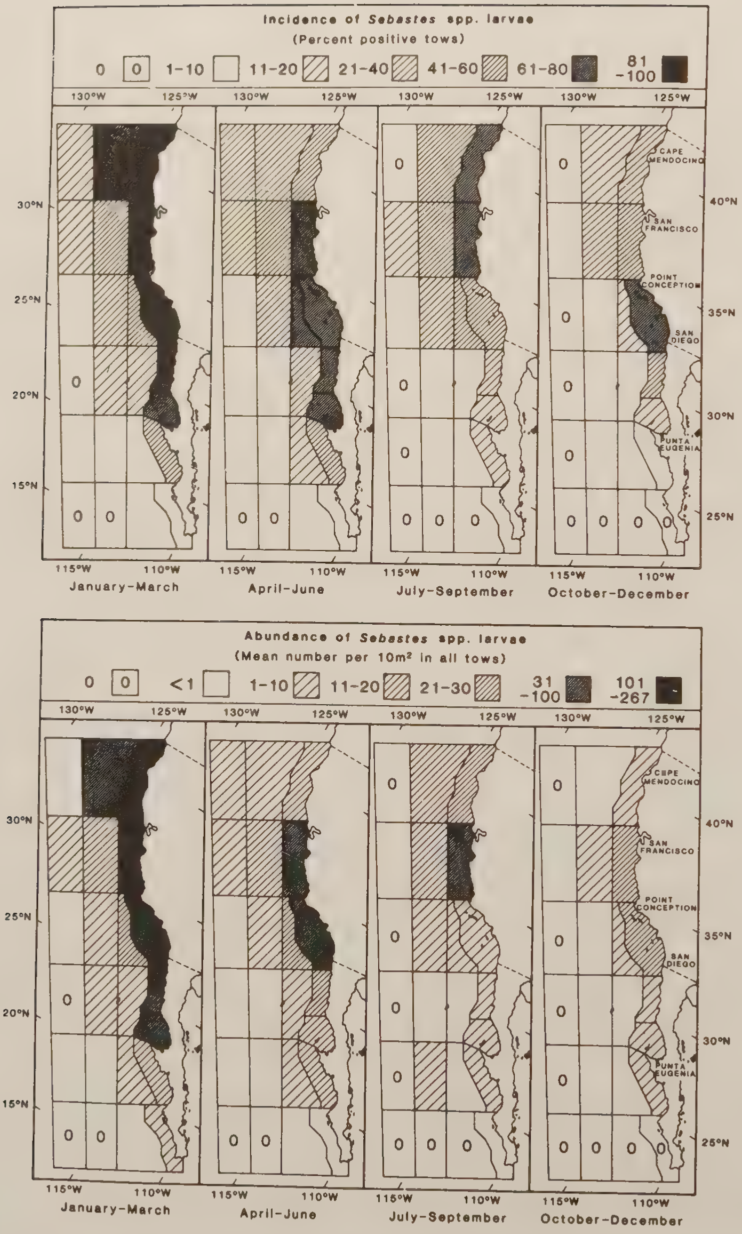
Incidence of Sebastes spp. larvae
(Percent positive tows)
0
1-10
11-20
21-40
41-60
61-80
81 -100
130°W
125°W
30°N
25°N
20°N
15°N
40°N
35°N
30°N
25°N
115°W
110°W
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
January-March
April-June
July-September
October-December
Abundance of Sebastes spp. larvae
(Mean number per 10m² in all tows)
0
<1
1-10
11-20
21-30
31 -100
101 -267

Fig. 4. Mean incidence (above) and abundance (below) of *Sebastes* spp. larvae in 23 CalCOFI regions sampled during 1951–1981.

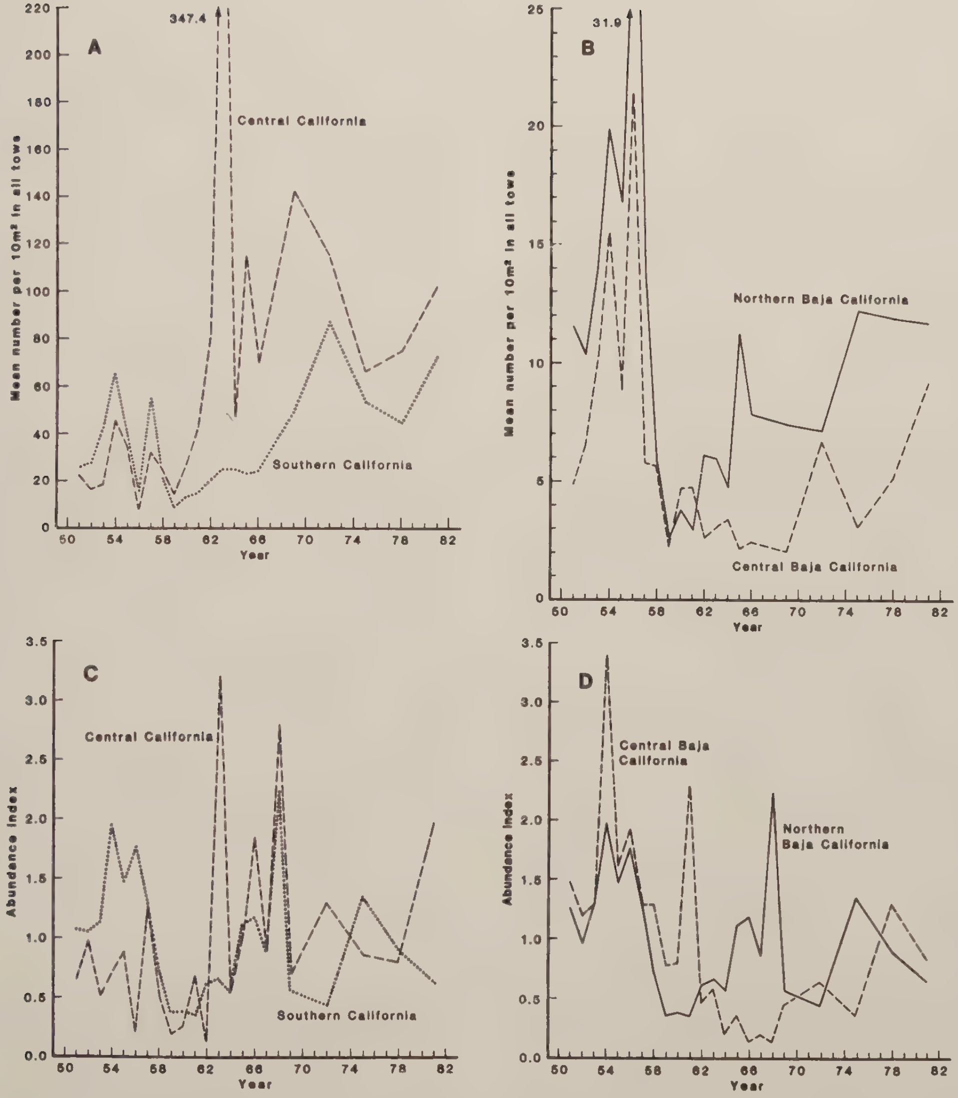

Fig. 5. Interannual variation in abundance of *Sebastes* spp. larvae in four coastal zones sampled on CalCOFI surveys off California and Baja California during 1951–1981. (A and B) mean annual abundances; (C and D) annual indices estimated by ANOVA techniques described by MacCall & Prager (1988).

dance was generally tenfold lower in Baja California (Fig. 5B) and contrasted sharply with that to the north. Values were relatively high in the 1950's until the 1958–1959 El Niño when there was a sharp decline. Abundance increased gradually in northern Baja California but remained low throughout the 1960's in central Baja California.

To compensate for uneven seasonal and areal coverage on annual CalCOFI surveys, an ANOVA method developed by MacCall & Prager (1988) was used to predict missing data and normalize interannual abundance values. Trends in ANOVA abundance indices (Fig. 5C, D) were similar to those derived from mean values (Fig. 5A, B). Depressed values during the 1957–1959 El Niño were evident for California and Baja California as was the strong peak in 1963 in central California (Fig. 5C, D). Indices for both central and southern California peaked in 1968 and then declined to near average values through most of the 1970's. In Baja California, indices declined sharply during the 1957–1959 El Niño and then showed opposite trends in northern and central Baja California. In 1961, a strong peak in central Baja California contrasted with a low index for northern Baja California; in 1968, a strong peak in northern Baja California coincided with an extremely low index for central Baja California.

Except for the depressed abundance during the 1958–1959 El Niño, when temperatures were high and zooplankton abundance was low, a relationship between interannual variation in environmental conditions (Chelton et al. 1982, Roesler & Chelton 1987) and abundance of *Sebastes* larvae is not evident. Trends and short-term shifts in abundance of larvae reflect fluctuations in biomass of dominant species and also variability in survival of early larvae. These result from vastly different interactions with physical and biotic environmental parameters and can only be understood by integrated studies of adult population processes and survival of larvae.

Study of abundance patterns of larvae for individual species has been impeded by the difficulty in identifying larvae (see Kendall 1991). Overall distribution patterns (Fig. 6) for species identified in CalCOFI plankton surveys are markedly different (Moser et al. 1977, 1985). Larvae of *S. aurora* and *S. paucispinis* have broad distributions from central Baja California to well north of the sampling region. *Sebastes jordani* larvae are more coastally and latitudinally confined, while *S. levis* larvae are restricted largely off the outer coast of southern California. *Sebastes macdonaldi* occurs primarily off Baja California. It is the only species of *Sebastes* whose adults and juveniles have been found there and in the Gulf of California; however, its larvae have not been reported from the latter (Moser 1972). *Sebastes cortezi* is an endemic species found along the chain of islands on the western side of the Gulf of California where strong tidal currents produce relatively low surface temperatures. The distributional differences among species contribute to the observed differences in seasonality of different geographic regions. Because different species probably respond to environmental features in different ways, it may be difficult to assess the role of environmental factors in interannual variation in abundance at the generic level (Fig. 5). MacGregor (1986) described seasonal and interannual abundance for larvae of four species (*S. paucispinis, S. jordani, S. levis* and *S. macdonaldi*) taken on several CalCOFI surveys. A complete description of any single species for the entire time series, however, awaits a comprehensive reexamination of CalCOFI samples containing *Sebastes* larvae.

Vertical distribution

The vertical distribution of *Sebastes* spp. larvae was described by Ahlstrom (1959) from 22 series of opening/closing nets taken at 15 stations off southern California and Baja California. Larvae were mainly in the upper mixed layer and within the thermocline but not below it; 97% were at depths shallower than 80 m, and 75% occurred between about 25 and 80 m depth. Boehlert et al. (1985) found a relatively shallower distribution for *Sebastes* spp. larvae off Oregon where the thermocline also was shallower (<30 m); 95% of the larvae were at less than 40 m, and 70% occurred within the 5–30 m range. Similarly, Sanchez & Acha (1988) found preflexion larvae of *S. oculatus* (*S. capensis*?)

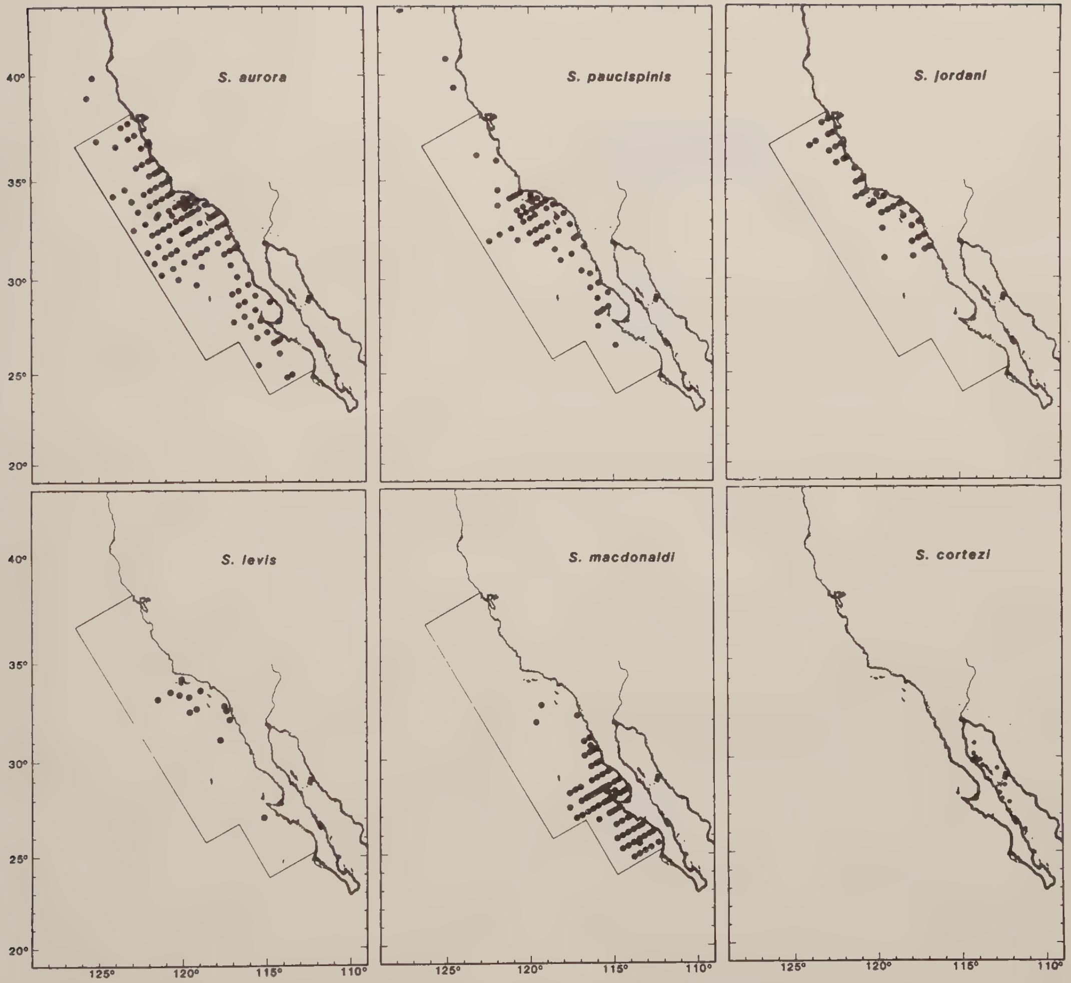

Fig. 6. Occurrences of larvae of six species of *Sebastes* on annual CalCOFI surveys (*S. aurora*, 1951–1981; *S. paucispinis*, 1953 and 1956; *S. jordani*, 1966; *S. levis*, 1951, 1955, 1968, 1969; *S. macdonaldi*, 1953, 1960, 1965, 1966; *S. cortezi*, 1956, 1957; area of frequent station occupancy is outlined; modified from Moser et al. 1977, 1985).

limited to the 10–30 m stratum over the Patagonian shelf. Kuwahara & Suzuki (1983) found an even shallower distribution of three species of *Sebastes* larvae in Wakasa Bay, Japan. More than 90% of the larvae of *S. marmoratus* and *S. pachycephalus*, and all *S. oblongus* larvae, occurred in the 0–25 m stratum. Approximately 63% of *S. marmoratus*, 87% of *S. pachycephalus* and 95% of *S. oblongus* were caught in surface tows.

Pommeranz & Moser (1987) reported on the distribution of eggs, embryos and larvae of northern anchovy, *Engraulis mordax*, taken in a series of 63 discrete depth tows at two stations off southern California in March-April 1980. Their shelf station was 2.4 nmi offshore over a bottom depth of about 350 m, and their offshore station (38.4 nmi offshore) was over a basin of about 1200 m depth. We analyzed catches of *Sebastes* larvae in these tows for the present paper. About 90% of the larvae of *Sebastes* spp. occurred at depths shallower than 80 m at both sta-

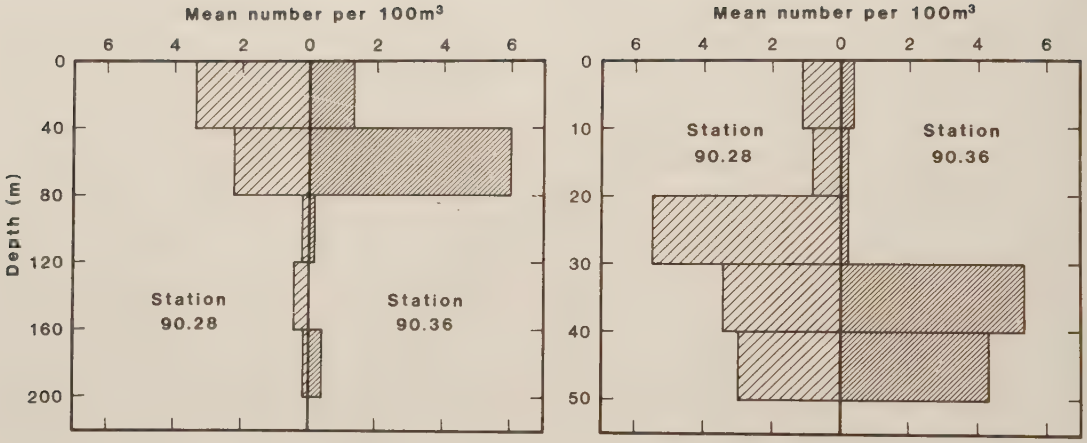

Fig. 7. Vertical distribution of *Sebastes* spp. larvae at two CalCOFI stations off southern California. Broad cross-hatching indicates the shelf station (Sta. 90.28) over a bottom depth of 350 m; narrow cross-hatching indicates the offshore station (Sta. 90.36) over a bottom depth of 1200 m.

tions (Fig. 7). The two stations differed markedly at the 20–30 m stratum; this stratum contained a large proportion of the total larvae at the shelf and virtually no larvae offshore. This difference corresponded with thermocline depth (about 20–40 m at the shelf station and 30–50 m at the offshore station). Interestingly, no larvae were taken at the surface at the offshore station, whereas the shelf station had a mean of 1.47 larvae per 100 m^3 in the neuston, 97% of these in the day hauls. About two-thirds of the mean volume of zooplankton in the upper 200 m was in the 0–80 m stratum, and the mean volume at the shelf station was about twice that at the offshore station. There was no clear relationship between mean zooplankton volume and mean densities of larvae; however, pump samples taken concurrently at the shelf station had peak concentrations of copepod nauplii in the 20–30 m stratum (Mullin et al. 1985).

Nearshore distribution

Information on the nearshore distribution of *Sebastes* spp. larvae is available from a 7-year ichthyoplankton survey off the San Onofre Nuclear Generating Station (SONGS) in California (W. Watson personal communication). This survey measured abundance patterns of fish larvae along a transect covering 6–75 m depth (Barnett et al. 1984, Walker et al. 1987). Based on these studies, the abundance of *Sebastes* spp. larvae has a strong seasonal pattern, with a winter-spring peak and a marked increase with increasing depth. The strong seasonal peak in abundance (Fig. 8) was restricted to a single month in 1978 (March) and 1979 (January). Such a narrow spawning peak in a restricted nearshore region could result from a smaller species complement compared with deeper, more speciose habitats. The two subsequent, small peaks could represent production of larvae from less abundant species or extrusion of multiple broods from an abundant species. Interestingly, three major kinds of *Sebastes* larvae were found in the samples.

In the onshore-offshore dimension, abundance increases abruptly at the shelf break to a mean of 32 larvae per 10 m^2 of sea surface (4.5 per 100 m^3; Fig. 9A). This agrees closely with the long-term mean (36 per 10 m^2) for CalCOFI samples off southern California (see Fig. 3C). Small numbers of larvae were found in the neuston and epibenthos (Fig. 9B), but highest densities were usually in midwater. This may change with growth, however, because all juveniles and most late-stage larvae occurred in surface samples (W. Watson personal communication).

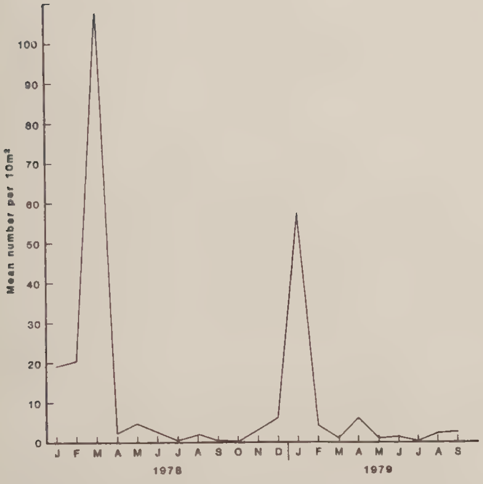

Fig. 8. Mean monthly abundance (number per 10 m^2) of *Sebastes* spp. larvae off San Onofre, California, during January 1978 to September 1979.

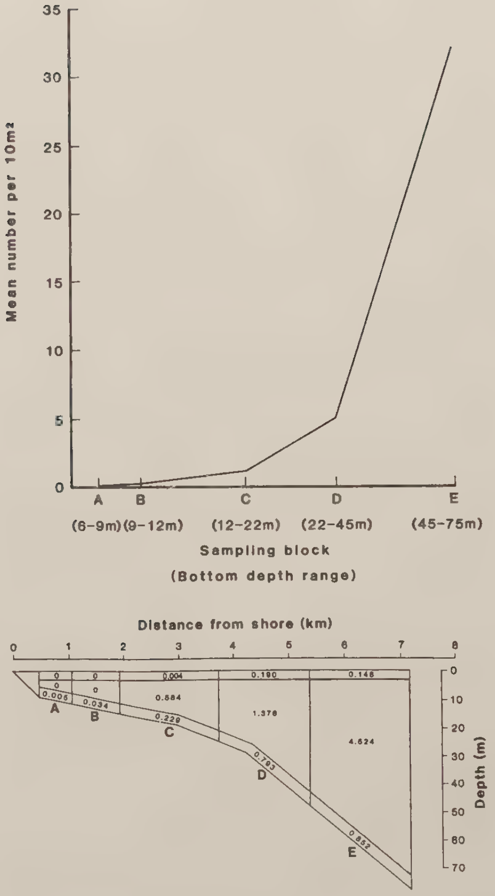

Fig. 9. Mean abundance and density of *Sebastes* spp. larvae on a transect off San Onofre, California, 1978–1983; (above) mean abundance (number per 10 m^2) for each sampling block and (below) mean density (number per 100 m^3) at surface, water column and epibenthos in each sampling block (shading highlights the stratum with the highest densities of larvae).

Ichthyoplankton assemblages

The relationship between *Sebastes* larvae and other ichthyoplankton has been examined in a number of analyses employing the recurrent group technique, a method that groups taxa based on their coincidence in time and space. When the CalCOFI time series from 1954 to 1960 was analyzed as a whole, *Sebastes* larvae were grouped with those of three abundant mesopelagic species and the Pacific hake, *Merluccius productus*, a demersal shelf and slope species (Moser et al. 1987). Analysis of individual years showed that *Sebastes* was also strongly associated with the northern anchovy, *Engraulis mordax*. A similar grouping was shown by Gruber et al. (1982) for a coastal survey in the Southern California Bight. In a survey off Washington, Oregon and northern California, Clark & Kendall (1985) showed that *Sebastes* larvae formed a group with the larvae of three deep-living flatfishes (*Glyptocephalus zachirus, Microstomus pacificus, Lyopsetta exilis*). *Sebastes* also had strong affinities with larvae of a group of mesopelagic species that contained two of the same species that were grouped with *Sebastes* larvae in the CalCOFI study. In bongo net collections from the northern Gulf of Alaska, *Sebastes* larvae were grouped with *G. zachirus* larvae and larvae of a genus of deep-living ronquils, *Bathymaster* spp.; the group formed by these species had strong affinities with two other flatfishes, the deep-living *Hippoglossoides elassodon* and the shallow-living *Psettichthys melanostictus* (Kendall & Dunn 1985). These studies generally support the contention of Richardson & Pearcy (1977) that *Sebastes* spp. larvae are distributed predominantly offshore.

Growth of larvae and juveniles

Growth rates of adult *Sebastes* are variable from species to species (Chen 1971), so it would not be surprising to find significant interspecific differences in the growth of larvae and juveniles. Boehlert & Yoklavich (1983) summarized data on growth of juvenile *Sebastes* species and noted greater than sixfold differences in laboratory experiments and nearly fourfold differences in field observations of growth. In the laboratory, growth is highly dependent upon temperature; average growth of newly settled *S. melanops* at 18° C was 3.4 times that at 7° C, although individual growth was a complex function of temperature, fish size and ration (Boehlert & Yoklavich 1983). The optimum temperature for growth for both *S. melanops* and *S. diploproa* (Boehlert 1981) shifts ontogenetically. Smaller fish grow fastest at higher temperatures, with a declining thermal optimum for growth with increasing size through the juvenile period. This is in keeping with the thermal ecology of many species, because younger juvenile fishes often select higher temperatures (Norris 1963).

Growth rates in the field integrate a range of environmental features and thus may be quite different from those in the laboratory. Several studies have measured growth in the field by counting otolith growth increments, which have been confirmed as daily in *S. melanops* by Yoklavich & Boehlert (1987). Studies using these techniques on larvae and pelagic juveniles of *Sebastes* demonstrated growth rates to be linear over the sizes measured (Fig. 10). The range of growth rates among species was as great as that measured in the laboratory, with the slowest measured for *Sebastes* spp. from the Atlantic (0.109 mm per day, Penney & Evans 1985) and the fastest for *S. paucispinis* (approximately 0.666 mm per day; D. Woodbury personal communication). *Sebastes jordani* has the second fastest growth observed (0.568 mm per day), despite having one of the smallest adult sizes in the genus.

Although juvenile growth rates measured in the laboratory have been comparable to those in the field, growth rates of larvae in laboratory rearing trials have not been as fast, especially with eastern North Pacific species. Kendall & Lenarz (1987) summarized rearing trials for seven species through 30–40 days and noted growth rates of 0.08–0.14 mm per day. These experiments cannot be considered characteristic of field growth, however, because mortality rates were typically very high and feeding conditions of larvae often less than optimum. This contrasts with the success of rearing *S. schlegeli* in Japan. Hoshiai (1977) noted growth rates of 0.385 mm per day in rearing trials of this species through 50–70 days of age. This species has a larger egg and larger size at parturition (6.89 mm) and thus rearing may be facilitated by the ability to use larger foods.

Feeding of larvae

Feeding has been examined for the planktonic larvae of several species of *Sebastes*. They appear to be diurnal feeders, and the percentage of larvae feeding decreases with increasing depth (Marak 1974). Sumida & Moser (1984) noted feeding during 0800–1600 Pacific standard time for *S. paucispinis*. They interpreted the decreasing stomach contents after this time to characterize a rapid evacuation rate (compared to gadoid larvae). Diurnal incidence of feeding in three species of *Sebastes* larvae from the nearshore waters of Japan was nearly 100% (Kuwahara & Suzuki 1983).

Generally, *Sebastes* larvae have been characterized as opportunistic feeders. Earliest larvae typically feed on copepod nauplii and to a lesser extent on invertebrate eggs, as confirmed in the North Atlantic (*Sebastes* spp., redfish complex; Bainbridge & McKay 1968, Marak 1974), in the western Pacific (*S. pachycephalus, S. marmoratus* and *S. oblongus*; Kuwahara & Suzuki 1983) and in the eastern Pacific (*S. paucispinis*; Sumida & Moser 1984). Larger larvae continue to feed on nauplii but also begin to take copepodites, adult copepods, euphausiids and limited numbers of other larger prey. Although most of the studies cited above observed an increase in the largest size of prey consumed with increasing growth, smaller prey items remain important in larger larvae, suggesting prey encounter rather than selectivity as the important feature of larval feeding in the genus (Kuwahara & Suzuki 1983). Bainbridge & McKay (1968) described the feeding of redfish and cod larvae; at equivalent sizes, the cod larvae took larger

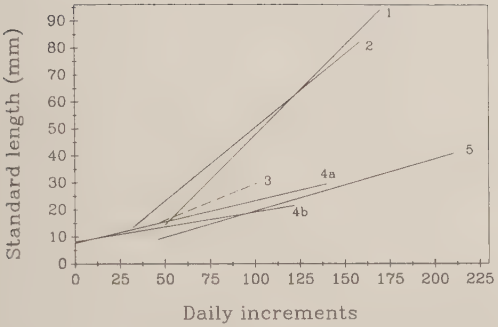

Fig. 10. Growth of field-collected pelagic *Sebastes* larvae and juveniles from studies using daily growth increments. In all cases, lines represent regressions within the bounds of length and age actually measured: 1 – *S. paucispinis* (D. Woodbury personal communication, N = 260); 2 – *S. jordani* (D. Woodbury personal communication, N = 302); 3 – *S. melanostomus* (Moser & Ahlstrom 1978, N = 4); 4a, b – Atlantic *Sebastes* spp. from 1980 and 1981, respectively (Penney & Evans 1985, N = 609, 539); 5 – *S. diploproa* (Boehlert 1981, N = 21).

prey items. Sumida & Moser (1984) compared feeding in *S. paucispinis* with that of another gadoid, *Merluccius productus*, and noted a similar phenomenon. At small sizes, *M. productus* larvae had larger mouths but continued to consume larger mean prey sizes than larvae of *S. paucispinis*, even after relative mouth size in the latter became greater than in *M. productus*. Although studies of feeding in pelagic juveniles have not been published, current research in central California suggests that pelagic juveniles remain opportunistic feeders, with significant dietary overlap between species (C. Reilly personal communication).

Pelagic juvenile habitats and transition to the benthic habitat

At transformation to pelagic juveniles, different strategies become apparent for different species; much of our information is inferential, however, for these larger sizes are typically more difficult to sample. Midwater trawls take a variety of species over a range of depths, including *S. saxicola, S. diploproa, S. proriger, S. jordani, S. goodei* (Berry & Perkins 1965), *S. macdonaldi* (Moser 1972), *S. melanostomus, S. aurora,* the subgenus *Sebastomus* (Moser & Ahlstrom 1978), *Sebastes crameri, S. helvomaculatus, S. pinniger* (Richardson & Laroche 1979), *S. auriculatus, S. caurinus, S. entomelas, S. flavidus, S. hopkinsi, S. levis, S. melanops, S. miniatus, S. mystinus, S. nigrocinctus, S. paucispinis, S. rastrelliger, S. semicinctus, S. serranoides, S. serriceps* and *S. wilsoni* (Kendall & Lenarz 1987). Other gear types sample in shallower waters; dip nets and purse seines have taken other species in association with drifting kelp. In the eastern Pacific, these have included *S. diploproa, S. paucispinis, S. rubrivinctus, S. serriceps, S. dallii* (Mitchell & Hunter 1970, Boehlert 1977) and, in the western Pacific, *S. thompsoni, S. vulpes* and *S. schlegeli* (Ikehara 1977). Brodeur & Pearcy (1986), using larger purse seines off Oregon and Washington, took 15 species of *Sebastes*. Species most frequently caught were *S. melanops, S. flavidus, S. mystinus, S. jordani* and *S. entomelas*.

Shallow-water residence

Residence in surface waters is known for pelagic juveniles of many species of *Sebastes*; those aggregating around drifting objects, however, typically occur within the upper meter of the ocean. Off southern California, Mitchell & Hunter (1970) sampled *S. diploproa* juveniles around drifting kelp, *Macrocystis pyrifera*, with a small purse seine, and Boehlert (1977) sampled them with small-mesh dip nets. Pelagic juveniles are present year-round, with the smallest sizes near 12 mm standard length (SL) but reaching sizes as great as 58.7 mm SL. Length frequencies suggest that the majority of recruitment of small individuals to the surface kelp habitat occurs from August to the following March (Boehlert 1977). Daily growth increment analysis suggests that the new recruits are approximately 60–70 days of age (Fig. 10); growth during the pelagic juvenile phase, at least to a length of 42 mm and ages of about 225 days, was nearly linear (Boehlert 1981).

The transition from pelagic to benthic juveniles in *S. diploproa* generally occurs at a size threshold of about 40 mm SL based upon the presence of benthic juveniles at depths down to 200 m. Although juveniles near the size threshold are present in surface waters nearly year-round, the surface-to-benthic migration occurs seasonally, generally from late spring to early summer (Boehlert 1977). Length-frequency analysis of surface and benthic specimens, however, suggests a 2-month hiatus between the disappearance of migratory surface fish and appearance of new, small benthic juveniles. This may involve a transitory midwater residence, although relatively few specimens have been taken there (Boehlert 1977). Surface specimens of *S. diploproa,* like many other species of *Sebastes*, are distributed far offshore from appropriate benthic habitat. Animals migrating to deep water in this offshore area would not reach bottom; instead, we propose that they reside in intermediate depths (Fig. 11). Recruitment to the nearshore is problematic in this case. In summer months off southern California, the general pattern of geostrophic flow at 250 m is to the northeast (Reid 1962); residence in this layer could facilitate coastward advection.

The surface living behavior of *S. diploproa* is a specialization of shallow-water residence. Recent studies indicate that pelagic juveniles of most species of *Sebastes* occupy the upper 100 m of the water column (Brodeur & Pearcy 1986, W. Lenarz personal communication). Preliminary evidence indicates that species occupy different depth strata within this zone; for example, *S. paucispinis* occurs in the 0–30 m stratum, *S. entomelas, S. flavidus* and *S. mystinus* occur in the 30–100 m stratum, while *S. goodei* and *S. hopkinsi* occupy the entire upper 100 m (W. Lenarz personal communication). Apparently depth stratification does not reflect specialized feeding habits and may be related to different mechanisms of settlement. Submergence to the 200 m zone of shoreward geostrophic flow could provide a mechanism for some species. Species occupying strata between 30 and 200 m could be carried in the shoreward subsurface flow that compensates for offshore Ekman transport during spring and summer (Sverdrup & Fleming 1941). Species that remain in the upper 30 m may be carried shoreward by flow reversals associated with the relaxation of upwelling or by compensating onshore flows related to upwelling filaments.

Midwater residence

Midwater residence following transformation has been shown for *S. melanostomus* (Moser & Ahlstrom 1978). Analysis of *Sebastes* juveniles captured in 217 midwater trawl samples taken over deep basins off southern California and Baja California revealed a recurring group of a few common types. Of these, *S. melanostomus* accounted for 16% and was distinguished by a remarkable pattern of melanistic bars, which alternated with transparent zones on the body and fins. Length-frequency distributions showed a size progression from April to October, and daily growth rings on otoliths of specimens taken from albacore, *Thunnus alalunga*, stomachs indicated that juveniles > 30 mm SL are 3–4 months old. Although most of the samples came from oblique integrated tows to various depths (maximum 1350 m), a series of 17 discrete depth tows showed *S. melanostomus* juveniles occupying the 200–250 m depth stratum. Thus, midwater residence, primarily at 200–250 m, would subject them to shoreward geostrophic flow similar to that hypothesized for the midwater juveniles of *S. diploproa.* The barred pigment pattern possibly serves to break up the body outline and camouflage the pelagic juveniles from predators. Disruptive pigmentation is characteristic of pelagic juveniles of *S. aurora*, the subgenus *Sebastomus* and *Sebastolobus altivelis*, which all co-occurred with *Sebastes melanostomus* (Moser & Ahlstrom 1978). *Sebastolobus altivelis* may recruit directly to the deep slope and basin habitats of the adults by descending vertically (Moser 1974). Further indirect evidence of a distinct midwater residence for some species of *Sebastes* is afforded by the results of a 6-year midwater trawl survey off central California (W. Lenarz personal communication). Pelagic juveniles of *S. melanostomus, S. aurora* and the subgenus *Sebastomus* were virtually absent from a series of > 500 midwater trawl samples taken during April-June 1983–1989. Sampling was restricted to the upper 100 m (mostly at 30 m depth), well above the depth occurrence of *Sebastes* species exhibiting midwater pelagic juvenile residence.

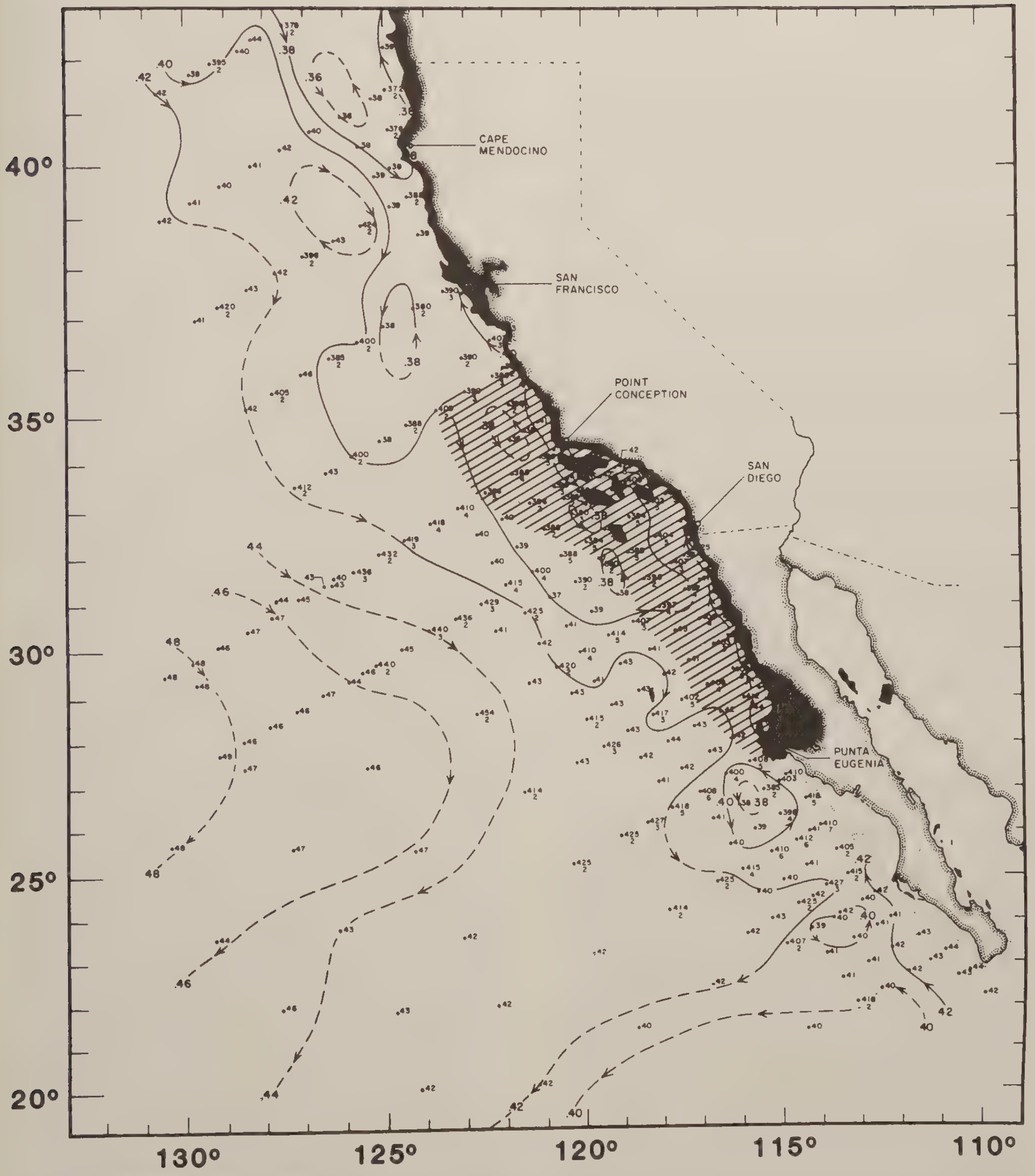
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
40°
35°
30°
25°
20°
130°
125°
120°
115°
110°

Fig. 11. Distribution of pelagic juvenile *S. diploproa* in central and southern California taken in surface collections (cross-hatched areas) in relation to mean geostrophic flow at 200 m depth during August 1950–1964; numbers indicate topography of the 200 decibar surface, in dynamic meters, relative to the 500 decibar surface; contour interval is 0.02 dynamic meter; darkened area along coast indicates appropriate benthic habitat for settlement (chart from Wyllie 1966).

Nearshore residence

The final hypothesized mechanism, and one perhaps most poorly known for *Sebastes*, is utilization of nearshore areas with minimum offshore dispersal. This has not been carefully investigated, because larvae are generally accepted to be important in offshore assemblages (Richardson & Pearcy 1977). Recent research on localized distributions of fish larvae (Marliave 1986) has resulted in new ideas about retention in the very nearshore zone, which is typically sampled poorly in ichthyoplankton investigations. Anderson (1983) suggested that certain nearshore species recruit to kelp canopy habitats as large larvae or very early juveniles at relatively young ages. This may also occur in Japanese species. Senta & Kinoshita (1985) noted the presence of small *S. inermis* in benthic nearshore stations. Many Japanese species are born at larger sizes than eastern North Pacific species; newly born *S. pachycephalus* are about 7 mm total length (TL) and are ready to settle to the bottom at an age of 25 days at 13 mm TL (Siokawa & Tsukahara 1961). This larger size at birth may facilitate the nearshore mechanism by minimizing the planktonic period.

Recruitment mechanisms

There is little question that *Sebastes* populations are characterized by significant interannual variability in recruitment strength, as suggested by abundance patterns of larvae (Fig. 5), juvenile recruitment (Mearns et al. 1980) and year-class strength differences after recruitment to the fishery (Norton 1987). The source of this recruitment variability could occur during several steps. First, reproductive output may vary from year to year within a species in response to food availability and environmental factors. Larson (1991) describes the dynamics of fat storage, which the female utilizes during the period of gestation (as opposed to the period of vitellogenesis observed in most fishes). Lenarz & Echeverria (1986) noted decreased fat deposition in El Niño years. Viviparous poeciliids may decrease the level of additional nutrition to embryos in times of adverse environmental conditions (Trexler 1985). This mechanism, if found in *Sebastes*, might explain either lower reproductive output or higher early mortality of smaller, less developed larvae, which would be consistent with the lower abundances of larvae during El Niño in the late 1950's (Fig. 5). The second source of recruitment variability would be mortality of larvae from either starvation or predation. Until improved species identification is possible, however, this source will be difficult to evaluate. Certainly species-specific responses to environmental and biotic effects differ (Norton 1987), and analysis based on generic-level characteristics will contribute relatively little to our understanding.

Advective sources of mortality for early larvae are suggested by the distant offshore distribution of *Sebastes* larvae and pelagic juveniles. There is some relationship between year-class strength variability and environmental conditions for at least some species; Norton (1987) suggested that successful year classes of widow rockfish, *S. entomelas*, may occur in years of increased onshore transport, possibly carrying pelagic larvae towards shore. This agrees with the ideas posed in Parrish et al. (1981). The vertical distribution of larvae, however, suggests that they are relatively rare in the shallow Ekman layer (Fig. 7) and may not be subject to offshore transport during upwelling. Moreover, the majority of offshore transport may occur through localized transport by jets (Mooers & Robinson 1984) or eddies (Simpson 1987). The latter may play an important role in the survival of *Sebastes* larvae and of other groundfishes that have been advected offshore. There is a remarkable overlap between the offshore field of mesoscale eddies (Lynn & Simpson 1987) and the zone of maximum concentration of copepod nauplii (Arthur 1977). As a result of high prey concentrations, larvae entrained to this zone could experience enhanced survival rather than increased mortality and offshore advection would be adaptive if linked with successful benthic recruitment of survivors. Further investigation of this hypothesis should focus on (1) the dynamics of phytoplankton, zooplankton and ichthyoplankton components of offshore eddies, (2) seasonal and interannual variations in the offshore eddy field and (3) the potential relationship of these variations with recruitment variations.

Localized eddies and other hydrographic features may be generated by headlands, seamounts and other complex topography (Boehlert & Genin 1987), and spawning in these areas might enhance retention of larvae. Hewitt (1981), for example, proposed that eddies play a role in speciation in the California Current region. On a smaller scale, potential retention areas associated with topography could result in subpopulations of some species (Iles & Sinclair 1982). If this mechanism exists for *Sebastes*, however, one would expect localized centers of enhanced or, conversely, depauperate benthic recruitment, as has been observed for sea urchins, *Strongylocentrotus purpuratus*, off the California coast (Ebert & Russell 1988). Studies of benthic juvenile recruitment will require a much broader geographic extent to evaluate this hypothesis.

Successful recruitment of pelagic juveniles to the benthic habitat may involve factors different from those affecting larvae. The pelagic juvenile phase may last several months to a year (Boehlert 1977). The broad distribution of pelagic juveniles relative to the area for possible settlement is evident in studies of albacore diets (Powell & Hildebrand 1950). Because the juvenile habitats of most species are poorly known, we cannot exclude the possibility that some species may have extended offshore distributions with concomitantly long pelagic juvenile phases. In purse seine collections, for example, Brodeur & Pearcy (1986) captured relatively large juveniles and adults of some species. Still, benthic recruitment of many species occurs with seasonal regularity (see Love et al. 1991) and thus is unlikely a stochastic process. Species such as *S. diploproa*, with a pelagic juvenile residence in surface waters, may use a shoreward transport mechanism such as that proposed by Shanks (1983). Species in midwater may use directed, shoreward swimming arising from avoidance of lower temperatures characteristic of fronts associated with passing internal waves, a mechanism suggested by Norris (1963) for *Girella nigricans*. Other directed movements such as orientation to magnetic or electric fields cannot be excluded. Comparative studies on species with different mechanisms will contribute a great deal to our understanding of settlement and recruitment in *Sebastes*.

Acknowledgements

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References cited

Ahlstrom, E.H. 1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish. Bull. 60: 107–146.

Ahlstrom, E.H. 1961. Distribution and relative abundance of rockfish (*Sebastodes* spp.) larvae off California and Baja California. Rapp. P.-V. Cons. Perm. Explor. Mer. 150: 169–176.

Ahlstrom, E.H., H.G. Moser & E.M. Sandknop. 1978. Distributional atlas of fish larvae in the California Current region: rockfishes, *Sebastes* spp., 1950 through 1975. Calif. Coop. Oceanic Fish. Invest. Atlas 26. 178 pp.

Ambrose, D., R.L. Charter, H.G. Moser & C.R. Santos Methot. 1987. Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1951. U.S. Dep. Commer., NOAA Tech. Memo., NMFS-SWFC-79. 196 pp.

Anderson, J.T. 1984. Early life history of redfish (*Sebastes* spp.) on Flemish Cap. Can. J. Fish. Aquat. Sci. 41: 1106–1116.

Anderson, T.W. 1983. Identification and development of nearshore juvenile rockfishes (genus *Sebastes*) in central California kelp forests. M.A. Thesis, California State University, Fresno. 216 pp.

Arthur, D.K. 1977. Distribution, size, and abundance of microcopepods in the California Current system and their possible influence on survival of marine teleost larvae. U.S. Fish. Bull. 75: 601–611.

Bainbridge, V. & G.A. Cooper. 1971. Populations of *Sebastes* larvae in the North Atlantic. Int. Comm. Northwest Atl. Fish. Res. Bull. 8: 27–35.

Bainbridge, V. & B.J. McKay. 1968. The feeding of cod and redfish larvae. Int. Comm. Northwest Atl. Fish. Spec. Publ. 7: 187–217.

Baranenkova, A.S. & N.S. Khokhlina. 1961. The distribution and size composition of larvae and young redfish in the Norwegian and Barents Seas. Rapp. P.-V. Cons. Perm. Explor. Mer. 150: 177–187.

Barnett, A.M., A.M. Jahn, P.D. Sertic & W. Watson. 1984. Distribution of ichthyoplankton off San Onofre, California, and methods for sampling very shallow coastal waters. U.S. Fish. Bull. 82: 97–111.

Berry, F.H. & H.C. Perkins. 1965. Survey of pelagic fishes of the California Current area. U.S. Fish Wildl. Serv., Fish. Bull. 65: 625–682.

Boehlert, G.W. 1977. Timing of the surface-to-benthic migration in juvenile rockfish, *Sebastes diploproa*, off southern California. U.S. Fish. Bull. 75: 887–890.

Boehlert, G.W. 1981. The effects of photoperiod and temperature on laboratory growth of juvenile *Sebastes diploproa* and a comparison with growth in the field. U.S. Fish. Bull. 79: 789–794.

Boehlert, G.W., D.M. Gadomski & B.C. Mundy. 1985. Vertical distribution of ichthyoplankton off the Oregon coast in spring and summer months. U.S. Fish. Bull. 83: 611–621.

Boehlert, G.W. & A. Genin. 1987. A review of the effects of seamounts on biological processes. pp. 319–334. *In*: B.H. Keating, P. Fryer, R. Batiza & G.W. Boehlert (ed.) Seamounts, Islands, and Atolls, Amer Geophys. Union, Geophysical Monograph 43.

Boehlert, G.W. & M.M. Yoklavich. 1983. Effects of temperature, ration, and fish size on growth of juvenile black rockfish, *Sebastes melanops*. Env. Biol. Fish. 8: 17–28.

Brodeur, R.D. & W.G. Pearcy. 1986. Distribution and relative abundance of pelagic nonsalmonid nekton off Oregon and Washington, 1979–1984. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 46. 85 pp.

Chelton, D.B., P.A. Bernal & J.A. McGowan. 1982. Large-scale interannual physical and biological interaction in the California Current. J. Mar. Res. 40: 1095–1125.

Chen, L.-C. 1971. Systematics, variation, distribution, and biology of rockfishes of the subgenus *Sebastomus* (Pisces, Scorpaenidae, *Sebastes*). Bull. Scripps Inst. Oceanogr. 18: 1–115.

Clark, J. & A.W. Kendall, Jr. 1985. Ichthyoplankton off Washington, Oregon, and northern California. Dept. of Commer., Nat. Mar. Fish. Serv., Northwest and Alaska Fisheries Center, Processed Rep. 85–10. 48 pp.

Ebert, T.A. & M.P. Russell. 1988. Latitudinal variation in size structure of the west coast purple sea urchin: a correlation with headlands. Limnol. Oceanogr. 33: 286–294.

Einarsson, H. 1961. The fry of *Sebastes* in Icelandic waters and adjacent seas. Rapp. P.-V. Cons. Perm. Explor. Mer. 150: 199–200.

Gruber, D., E.H. Ahlstrom & M.M. Mullin. 1982. Distribution of ichthyoplankton in the Southern California Bight. Calif. Coop. Oceanic Fish. Invest. Rep. 23: 172–179.

Guillemot, P.J., R.J. Larson & W.H. Lenarz. 1985. Seasonal cycles of fat and gonad volume in five species of northern California rockfish (Scorpaenidae: *Sebastes*). U.S. Fish. Bull. 83: 299–311.

Harada, E. 1962. A contribution to the biology of the black rockfish, *Sebastes inermis* (Cuvier et Valenciennes). Publ. Seto Mar. Biol. Lab. 5: 307–361.

Henderson, G.T.D. 1961. Continuous plankton records: the distribution of young *Sebastes marinus*. Bull. Mar. Ecol. 5: 173–193.

Hewitt, R. 1981. Eddies and speciation in the California Current. Calif. Coop. Oceanic Fish. Invest. Rep. 22: 96–98.

Hewitt, R.P. 1988. Historical review of the oceanographic approach to research. Calif. Coop. Oceanic Fish. Invest. Rep. 29: 27–41.

Hoshiai, G. 1977. Larvae and juveniles of the scorpaenid fish, *Sebastes schlegeli*. Jap. J. Ichthyol. 24: 35–42. (in Japanese).

Ikehara, K. 1977. Studies on the fish eggs and larvae accompanied with drifting seaweeds in the Sado Strait and its vicinity. Bull. Jap. Sea Reg. Fish. Res. Lab. 28: 17–28. (in Japanese).

Iles, T.D. & M. Sinclair. 1982. Atlantic herring: stock discreteness and abundance. Science 215: 627–633.

Kendall, A.W., Jr. 1991. Systematics and identification of larvae and juveniles of the genus *Sebastes*. Env. Biol. Fish. 30: 173–190.

Kendall, A.W., Jr. & J. Clark. 1982. Ichthyoplankton off Washington, Oregon, and northern California, April-May 1980. Dept. of Commer., Nat. Mar. Fish. Serv., Northwest and Alaska Fisheries Center, Processed Rep. 82–11. 44 pp.

Kendall, A.W., Jr. & J.R. Dunn. 1985. Ichthyoplankton of the continental shelf near Kodiak Island, Alaska. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 20. 89 pp.

Kendall, A.W., Jr. & P. Ferraro. 1988. Ichthyoplankton of the Gulf of Alaska near Kodiak Island, March to June 1985. Dept. of Commer., Nat. Mar. Fish. Serv., Northwest and Alaska Fisheries Center, Processed Rep. 88–03. 88 pp.

Kendall, A.W., Jr. & W.H. Lenarz. 1987. Status of early life history studies of Northeast Pacific rockfishes. pp. 99–128. *In*: Proceedings of the International Rockfish Symposium, Anchorage, Alaska, Univ. Alaska, Alaska Sea Grant Rep. 87–2.

Kim, J.M., J.M. Yoo, H.T. Huh & S.S. Cha. 1985. Distribution of fish larvae in the Ulsan Bay, South Korea and its adjacent waters. Ocean Res. (Seoul) 7: 15–22.

Kuwahara, A. & S. Suzuki. 1983. Vertical distribution and feeding of three species of rockfish Scorpaenidae larvae. Bull. Jap. Soc. Sci. Fish. 49: 515–520. (in Japanese).

Larson, R.J. 1991. Seasonal cycles of reserves in relation to reproduction in *Sebastes*. Env. Biol. Fish. 30: 57–70.

LeBrasseur, R. 1970. Larval fish species collected in zooplankton samples from the northeastern Pacific Ocean 1956–1959. Fish. Res. Board Can. Tech. Rep. 175. 47 pp.

Lenarz, W.H. & T.W. Echeverria. 1986. Comparison of visceral fat and gonadal fat volumes of yellowtail rockfish, *Sebastes flavidus*, during a normal year and a year of El Niño conditions. U.S. Fish. Bull. 84: 743–745.

Lisovenko, L.A. 1967. Distribution of the larvae of rockfish (*Sebastodes alutus* Gilbert) in the Gulf of Alaska. pp. 217–225. *In*: P.A. Moiseev (ed.) Soviet Fisheries Investigations in the Northeast Pacific, Part III, U.S. Dep. Commer., Clearinghouse Fed. Sci. Tech. Inform., Springfield.

Loeb, V.J. & O. Rojas. 1988. Interannual variation of ichthyoplankton composition and abundance relations off northern Chile, 1964–85. U.S. Fish. Bull. 86: 1–24.

Love, M.S., M.H. Carr & L.J. Haldorson. 1991. The ecology of substrate-associated juveniles of the genus *Sebastes*. Env. Biol. Fish. 30: 225–243.

Lynn, R.J. & J.J. Simpson. 1987. The California Current system: the seasonal variability of its physical characteristics. J. Geophysical Res. 92: 12947–12966.

MacCall, A.D. & M.H. Prager. 1988. Historical changes in abundance of six fish species off southern California, based on CalCOFI egg and larva samples. Calif. Coop. Oceanic Fish. Invest. Rep. 29: 91–101.

MacGregor, J.S. 1970. Fecundity, multiple spawning, and description of the gonads in *Sebastodes*. U.S. Fish. Wildl. Serv. Spec. Sci. Rep. Fish. 596. 12 pp.

MacGregor, J.S. 1986. Relative abundance of four species of *Sebastes* off California and Baja California. Calif. Coop. Oceanic Fish. Invest. Rep. 27: 121–135.

Marak, R.R. 1974. Food and feeding of larval redfish in the Gulf of Maine. pp. 267–275. *In*: J.H.S. Blaxter (ed.) The Early Life History of Fish, Springer-Verlag, New York.

Marliave, J.B. 1986. Lack of planktonic dispersal of rocky intertidal fish larvae. Trans. Amer. Fish. Soc. 115: 149–154.

Mearns, A.J., M.J. Allen, M.D. Moore & M.J. Sherwood. 1980. Distribution, abundance, and recruitment of soft-bottom rockfishes (Scorpaenidae: *Sebastes*) on the southern California mainland shelf. Calif. Coop. Oceanic Fish. Invest., Rep. 21: 180–191.

Mitchell, C.T. & J.R. Hunter. 1970. Fishes associated with drifting kelp, *Macrocystis pyrifera*, off the coast of southern California and northern Baja California. Calif. Fish Game 56: 288–297.

Mooers, C.N.K. & A.R. Robinson. 1984. Turbulent jets and eddies in the California Current and inferred cross-shore transports. Science 223: 51–53.

Moser, H.G. 1967. Reproduction and development of *Sebastodes paucispinis* and comparison with other rockfishes off southern California. Copeia 1967: 773–797.

Moser, H.G. 1972. Development and geographic distribution of the rockfish, *Sebastes macdonaldi* (Eigenmann and Beeson, 1893), family Scorpaenidae, off southern California and Baja California. U.S. Fish. Bull. 70: 941–958.

Moser, H.G. 1974. Development and distribution of larvae and juveniles of *Sebastolobus* (Pisces: family Scorpaenidae). U.S. Fish. Bull. 72: 865–884.

Moser, H.G. & E.H. Ahlstrom. 1978. Larvae and pelagic juveniles of blackgill rockfish, *Sebastes melanostomus*, taken in midwater trawls off southern California and Baja California. J. Fish. Res. Board Can. 35: 981–996.

Moser, H.G., E.H. Ahlstrom & E.M. Sandknop. 1977. Guide to the identification of scorpionfish larvae (family Scorpaenidae) in the eastern Pacific with comparative notes on species of *Sebastes* and *Helicolenus* from other oceans. U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 402. 71 pp.

Moser, H.G. & J.L. Butler. 1981. Description of reared larvae and early juveniles of the calico rockfish, *Sebastes dallii* (Eigenmann and Beeson 1894). Calif. Coop. Oceanic Fish. Invest. Rep. 2: 88–95.

Moser, H.G., E.M. Sandknop & D.A. Ambrose. 1985. Larvae and juveniles of aurora rockfish, *Sebastes aurora,* from off California and Baja California. pp. 55–64. *In*: A.W. Kendall, Jr. & J.B. Marliave (ed.) Descriptions of Early Life History Stages of Selected Fishes: From the 3rd International Symposium on the Early Life History of Fishes and 8th Annual Larval Fish Conference, Can. Tech. Rep. Fish. Aquat. Sci. 1359.

Moser, H.G., P.E. Smith & L.E. Eber. 1987. Larval fish assemblages in the California Current region, 1954–60, a period of dynamic environmental change. Calif. Coop. Oceanic Fish. Invest. Rep. 28: 97–127.

Mullin, M.M., E.R. Brooks, F.M.H. Reid, J. Napp & E.F. Stewart. 1985. Vertical structure of nearshore plankton off southern California: a storm and a larval fish food web. U.S. Fish. Bull. 83: 151–170.

Norris, K.S. 1963. The functions of temperature in the ecology of the percoid fish *Girella nigricans* (Ayres). Ecol. Monogr. 33: 23–62.

Norton, J. 1987. Ocean climate influences on groundfish recruitment in the California Current. pp. 73–99. *In*: Proceedings of the International Rockfish Symposium, Anchorage, Alaska, Univ. Alaska, Alaska Sea Grant Rep. 87–2, Anchorage.

Okiyama, M. 1965. A preliminary study of the fish eggs and larvae occurring in the Sado Strait, Japan Sea, with some remarks on the vertical distribution of some fishes. Bull. Jap. Sea. Reg. Fish. Lab. 15: 13–37. (in Japanese).

Parrish, R.H., C.S. Nelson & A. Bakun. 1981. Transport mechanisms and reproductive success of fishes in the California Current. Biol. Oceanogr. 1: 175–203.

Penney, R.W. & G.T. Evans. 1985. Growth histories of larval redfish (*Sebastes* spp.) on an offshore Atlantic fishing bank determined by otolith increment analysis. Can. J. Fish. Aquat. Sci. 42: 1452–1464.

Pommeranz, T. & H.G. Moser. 1987. Data report on the vertical distribution of the eggs and larvae of northern anchovy, *Engraulis mordax*, at two stations in the Southern California Bight, March-April, 1980. U.S. Dep. Commer., NOAA Tech. Memo., NMFS-SWFC-75. 140 pp.

Powell, D.E. & H.H. Hildebrand. 1950. Albacore tuna exploration in Alaskan and adjacent waters, 1949. U.S. Fish Wildl. Ser. Fish. Leafl. 376. 33 pp.

Reid, J.L., Jr. 1962. Measurements of the California countercurrent at a depth of 250 meters. J. Mar. Res. 20: 134–137.

Reid, J.L., G.I. Roden & J.G. Wyllie. 1958. Studies of the California Current system. Calif. Coop. Oceanic Fish. Invest. Rep. 6: 27–57.

Richardson, S.L. & W.A. Laroche. 1979. Development and occurrence of larvae and juveniles of the rockfishes *Sebastes crameri, Sebastes pinniger*, and *Sebastes helvomaculatus* (family Scorpaenidae) off Oregon. U.S. Fish. Bull. 77: 1–46.

Richardson, S.L., J.L. Laroche & M.D. Richardson. 1980. Larval fish assemblages and associations in the north-east Pacific Ocean along the Oregon coast, winter-spring 1972–1975. Estuarine Coastal Mar. Sci. 11: 671–699.

Richardson, S.L. & W.G. Pearcy. 1977. Coastal and oceanic fish larvae in an area of upwelling off Yaquina Bay, Oregon. U.S. Fish. Bull. 75: 125–145.

Roesler, C. & D.B. Chelton. 1987. Zooplankton variability in the California Current, 1951–1982. Calif. Coop. Oceanic Fish. Invest. Rep. 28: 59–96.

Sanchez, R.P. & E.M. Acha. 1988. Development and occurrence of embryos, larvae and juveniles of *Sebastes oculatus* with reference to two Southwest Atlantic scorpaenids: *Helicolenus dactylopterus lahillei* and *Pontinus rathbuni*. Meeresforsch. 32: 107–133.

Senta, T. 1962. Studies on the occurrence of eggs and larvae of fishes in adjacent waters to the Oki Islands. Jap. J. Ecol. 12: 152–166. (in Japanese).

Senta, T. & I. Kinoshita. 1985. Larval and juvenile fishes occurring in surf zones of western Japan. Trans. Amer. Fish. Soc. 114: 608–618.

Shanks, A.L. 1983. Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. Mar. Ecol. Prog. Ser. 13: 311–315.

Shenker, J.M. 1988. Oceanographic associations of neustonic larval and juvenile fishes and Dungeness crab megalopae off Oregon. U.S. Fish. Bull. 86: 299–317.

Simpson, J.J. 1987. Transport processes affecting the survival of pelagic fish stocks in the California Current. Amer. Fish. Soc. Symp. 2: 39–60.

Siokawa, T. & H. Tsukahara. 1961. Studies on habits of coastal fishes in the Amakusa Islands. Part I. Early life history of the purple rockfish, *Sebastes pachycephalus pachycephalus* Temminck et Schlegel. Rec. Oceanogr. Works Japan. Spec. 5: 123–127.

Smith, P.E. & H.G. Moser. 1988. CalCOFI time series: an overview of fishes. Calif. Coop. Oceanic Fish. Invest. Rep. 29: 66–78.

Sorokin, V.P. 1961. The redfish; gametogenesis and migrations of the *Sebastes marinus* (L.) and *Sebastes mentella* Travin. Rapp. P.-V. Cons. Perm. Int. Explor. Mer. 150: 245–250.

Sumida, B.Y. & H.G. Moser. 1984. Food and feeding of bocaccio (*Sebastes paucispinis*) and comparison with Pacific hake (*Merluccius productus*) larvae in the California Current. Calif. Coop. Oceanic Fish. Invest. Rep. 25: 112–118.

Sverdrup, H.U. & R.H. Fleming. 1941. The waters off the coast of southern California, March to July, 1937. Bull. Scripps Inst. Oceanogr. 4: 261–378.

Tåning, A.V. 1949. On the breeding places and abundance of the redfish (*Sebastes*) in the North Atlantic. J. Cons. Int. Explor. Mer. 16: 85–95.

Templeman, W. 1959. Redfish distribution in the North Atlantic. Bull. Fish. Res. Board Can. 120. 173 pp.

Trexler, J.C. 1985. Variation in the degree of viviparity in the sailfin molly, *Poecilia latipinna*. Copeia 1985: 999–1004.

Waldron, K.D. 1972. Fish larvae collected from the northeastern Pacific Ocean and Puget Sound during April and May, 1967. U.S. Dep. Commer., NOAA Tech. Rep., NMFS-SSRF-663. 16 pp.

Waldron, K.D. 1981. Ichthyoplankton. pp. 471–493. *In*: D.W. Hood & J.A. Calder (ed.) The Eastern Bering Sea Shelf: Oceanography and Resources, U.S. Gov. Print. Off., Washington, D.C.

Walker, H.J., Jr., W. Watson & A.M. Barnett. 1987. Seasonal occurrence of larval fishes in the nearshore Southern California Bight off San Onofre, California. Estuarine Coastal Shelf Sci. 25: 91–109.

Wyllie, J.G. 1966. Geostrophic flow of the California Current at the surface and at 200 meters. Calif. Coop. Oceanic Fish. Invest., Atlas 4. xii + 288 pp.

Wyllie Echeverria, T. 1987. Thirty-four species of California rockfishes: maturity and seasonality of reproduction. U.S. Fish. Bull. 85: 229–250.

Yoklavich, M.M. & G.W. Boehlert. 1987. Daily growth increments in otoliths of juvenile black rockfish, *Sebastes melanops*: an evaluation of autoradiography as a new method of validation. U.S. Fish. Bull. 85: 826–832.

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CHAPTER EIGHT

SOME NEW AND POTENTIAL USES OF DENTAL LAYERS IN STUDYING DELPHINID POPULATIONS

Albert C. Myrick, Jr.

INTRODUCTION

Ever since the discovery by Nishiwaki and Yagi (1953) that it is possible to estimate the age of a dolphin by analyzing the layers in a single tooth, scientists have used tooth ages in conjunction with other data to conduct their biological investigations of dolphins (see Scheffer and Myrick 1980). By studying enough tooth samples from animals taken in the field, it is possible to identify important age-related characteristics of whole dolphin populations, such as the age structure of the population, the average age at sexual maturity (determined from reproductive organs and tooth layer counts), and the average reproductive longevity. This information can then be used, along with data derived from pregnancy and mortality rates, to assess the current condition of a given population and predict its future growth rates. Such assessments become particularly valuable for populations jeopardized by direct hunting, by alteration of their habitat, or by inadvertent kill through entanglement in or entrapment by fishing gear.

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Thousands of dolphins are killed incidentally each year in the eastern tropical Pacific (ETP) when purse seines are set on dolphin schools to capture yellowfin tuna that associate with them (Perrin 1969; Smith 1983; Hammond and Tsai 1983). In 1972, concern over the biological consequences of this considerable annual mortality prompted the U.S. National Marine Fisheries Service to mount a long-term monitoring and research program to study the problem.

In 1978, I began work on the problem of trying to estimate ages from burgeoning samples of teeth collected from the kill by federal technicians aboard selected ETP seiners. To extract age or other biological information from layers in dolphin teeth requires a certain basic understanding of the teeth, such as which tooth to use, when the tooth tissues are formed, how and where layers are accumulated, what factors may affect layer deposition, how they appear when viewed microscopically, where in the layered tissue to begin making a tooth age reading, and what the layers represent in terms of time.

THE UNIQUE TEETH OF DOLPHINS

Teeth of dolphins are different from those in any other mammal group in a number of important respects. First, except for the rodents and lagomorphs (pikas, rabbits, and hares), in which teeth are highly modified for gnawing and grinding, and the edentates and allies (pangolins, some anteaters, sloths, and armadillos), in which teeth are strongly reduced or absent, almost all toothed mammals produce baby or milk teeth and adult or permanent teeth (Scott and Symons 1964; Peyer 1968; Walker 1968). Dolphins produce only a permanent set of teeth: in a dolphin, the teeth form before birth, erupt within a few months after birth, and remain in place throughout its life.

Second, with the exception of the Amazon River dolphin (*Inia geoffrensis*), whose rear teeth are almost molarlike, and a few species in which teeth have undergone retrogression (*Phocoenoides* sp.) or reduction (narwhals and beaked whales), virtually all dolphins have homodont dentition, that is, all teeth of an individual have one shape—usually simple cones or pegs. Homodonty is common in fish, amphibians, and reptiles, but among the mammals, it is limited only to toothed whales and dolphins. Most mammals have heterodont dentition, with teeth differentiated into incisors, canines, premolars, and molars, or some combination of two or more types (Peyer 1968).

Another feature peculiar to dolphin teeth is that they are far more numerous in most delphinid species than in any other mammals with nor-

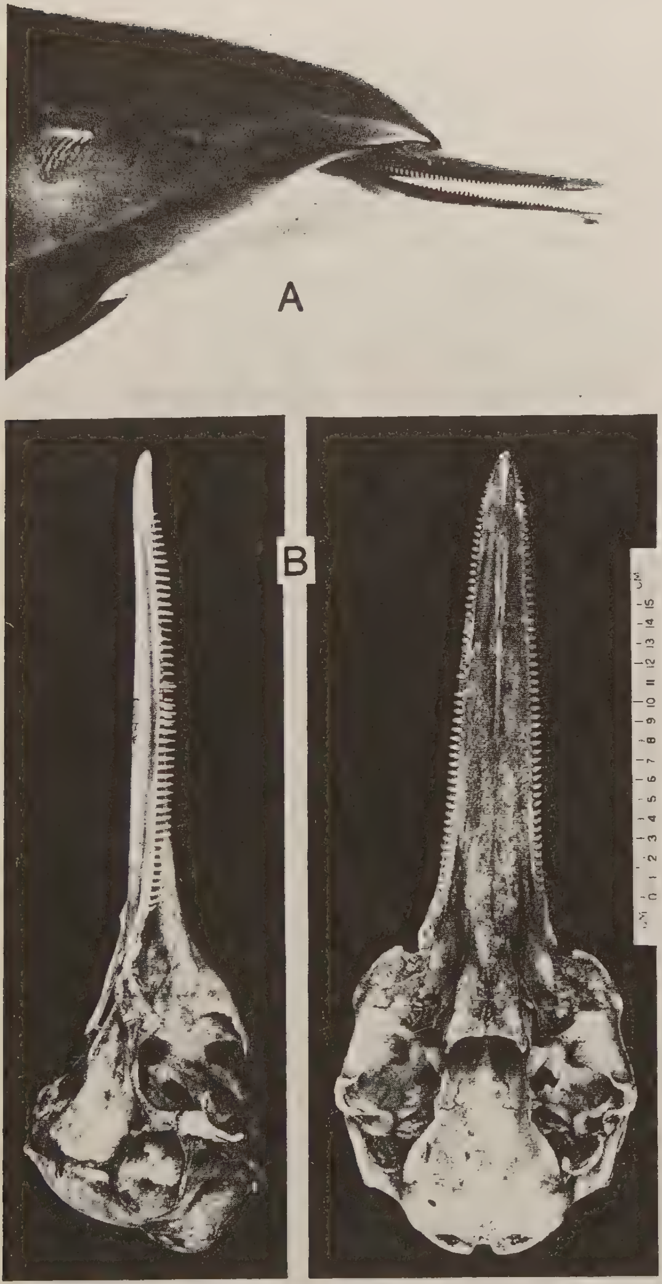
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Fig. 8.1. Reiterative homodont teeth in dolphins. A. Head of spinner dolphin (*Stenella longirostris*) showing numerous teeth in upper and lower jaws. B. Right lateral and ventral aspects of a spinner dolphin skull, showing teeth. (Photo from Perrin 1972.)

mal teeth. Humans have 7 or 8 teeth on each side of both upper and lower jaws. Primitive placental mammals have 11 on a side, with a total of 44. But (to take one of the extreme examples) among spinner dolphins (*Stenella longirostris*), individuals may have a total of between 180 and 220 teeth, arranged in rows of at least 45 teeth on each side of each jaw (fig. 8.1). Among other living mammals, only the African dog (*Otocyon megalotis*), with a heterodont series of up to 50 rather weak teeth (Peyer 1968), and the giant armadillo (*Priodontes giganteus*), with up to 100 intermittently shed teeth (Scott and Symons 1964, Walker 1968), show any trend toward this kind of dental reiteration.

SOME DENTAL ANATOMY

A dolphin tooth is a natural recording device, somewhat like a trunk of a tree that registers changes through its own life by the characteristics of its accumulating rings. The tooth differs from trees, however, in having three layering tissues instead of one. Each tissue, enamel, dentine, and cementum, is deposited in incremental layers, apparently with clockworklike regularity (fig. 8.2). In small delphinid species, deposition of enamel, which forms the apical mantle of the tooth, probably commences in the fetus three or four months after conception and is completed shortly before the dolphin's birth (Myrick 1980). The layers of enamel appear to represent daily increments (ibid., Boyde 1980; fig. 8.3).

The body of the tooth is composed of layers of dentine formed by continuous application of the tissue to the inner surface of the hollow dental cone. Dentine deposition begins concurrently with the onset of enamel formation, and thus, like enamel, prenatal dentine represents a record of a large part of the fetal life. However, unlike enamel, which forms prominent daily layers, prenatal dentinal layers show what seems to be a monthly depositional pattern (Myrick 1984*b*, Myrick et al. 1984).

Dentine deposited after birth, that is, postnatal dentine, is more conspicuously layered than prenatal dentine. As in most other mammals, postnatal dentinal deposition in dolphins begins at birth with the formation of a distinctive hypomineralized *neonatal layer* on the inner surface of the prenatal dentine (fig. 8.2). Formation of dentine usually slows down and gradually stops in most mammals but probably not in most dolphins. Postnatal dentinal layers in dolphins continue to accumulate internally until death or until the pulp cavity fills with dentine sufficiently to close off the supply of nutrients to the dentine-producing cells. Unless factors alter a dolphin's calcium or protein physiology sufficiently to interfere with the layering process, dentinal layers, from the neonatal layer to the pulp cavity margin, represent the dolphin's complete postnatal depo-

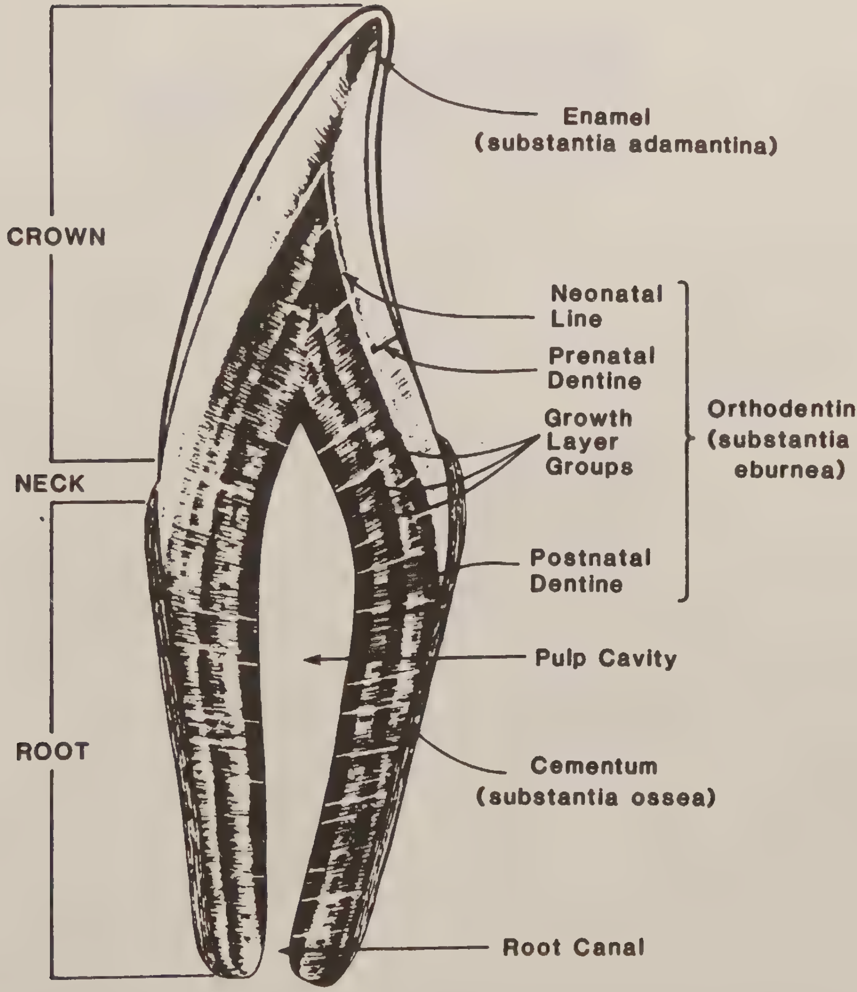
CROWN
NECK
ROOT
Enamel (substantia adamantina)
Neonatal Line
Prenatal Dentine
Growth Layer Groups
Orthodentine (substantia eburnea)
Postnatal Dentine
Pulp Cavity
Cementum (substantia ossea)
Root Canal

Fig. 8.2. Sketch of typical dolphin tooth in thin section showing tissues and general anatomy (from Perrin and Myrick 1980).

sitional record. Of course, the dentinal record would be truncated if the dolphin lived beyond the time of pulp-cavity occlusion.

Formation of cemental layers begins shortly after birth. Succeedingly younger layers of this tissue are applied to the external surface of the tooth's basal half. Because deposition occurs externally in the relatively unconfined space of the tooth socket, or alveolus, accumulation of cemental layers is thought to continue until death. This tissue should represent an uninterrupted layered recording of the entire postnatal life, presuming again that there is no sustained physiological interference.

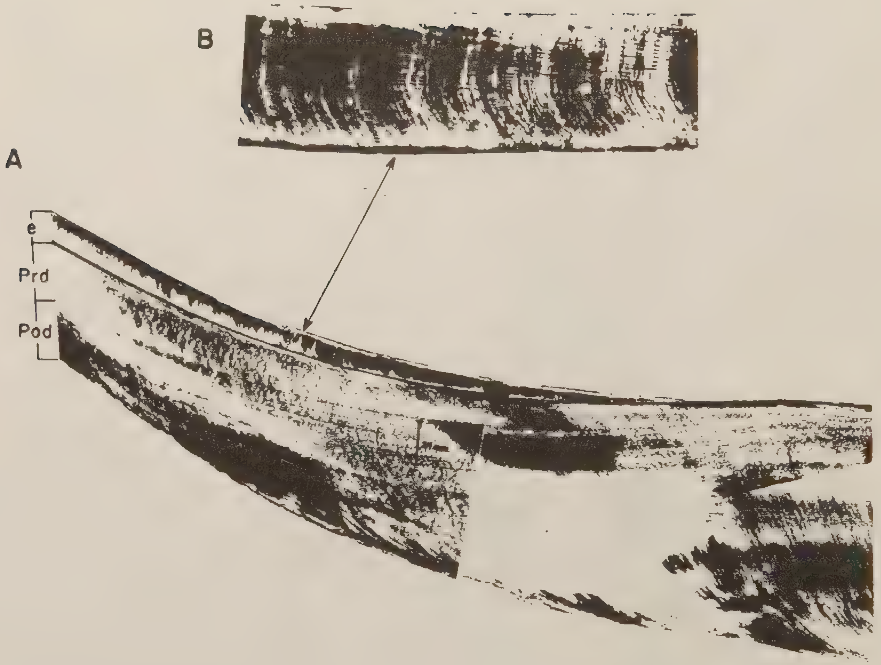

Fig. 8.3. Daily (?) layering in enamel in a tooth of a spotted dolphin (*Stenella attenuata*). A. Half of a tooth section viewed with polarized light and showing layering in the enamel (arrow). B. Highly magnified section of enamel as shown in A showing layers as indicated by marks. Because of the oblique (off-lapping) arrangement of layers, many transects at various intervals from apex to neck may be necessary to obtain full counts. A total of 223 enamel layers was seen in tooth depicted. Abbreviations: e, enamel; Prd, prenatal dentine; Pod, postnatal dentine. (From Myrick 1980.)

As a corollary of the dolphin's homodont and reiterative dentition, deposition of the layered record in one tooth occurs at the same time, in the same sequence, and with virtually identical patterns as in almost every other tooth in a dolphin's jaws (Myrick et al. 1984). This means that the number and distinctness of dentinal layers identified in one tooth will be the same as those in adjacent teeth. More important, it indicates that all of the teeth are under complete systemic control. The subtle uniqueness of the layering pattern is so well replicated in each tooth of an individual that by comparing the layering patterns of two teeth, even if they have the same number of layers, I have usually been able to determine whether or not they were taken from the same specimen (fig. 8.4).

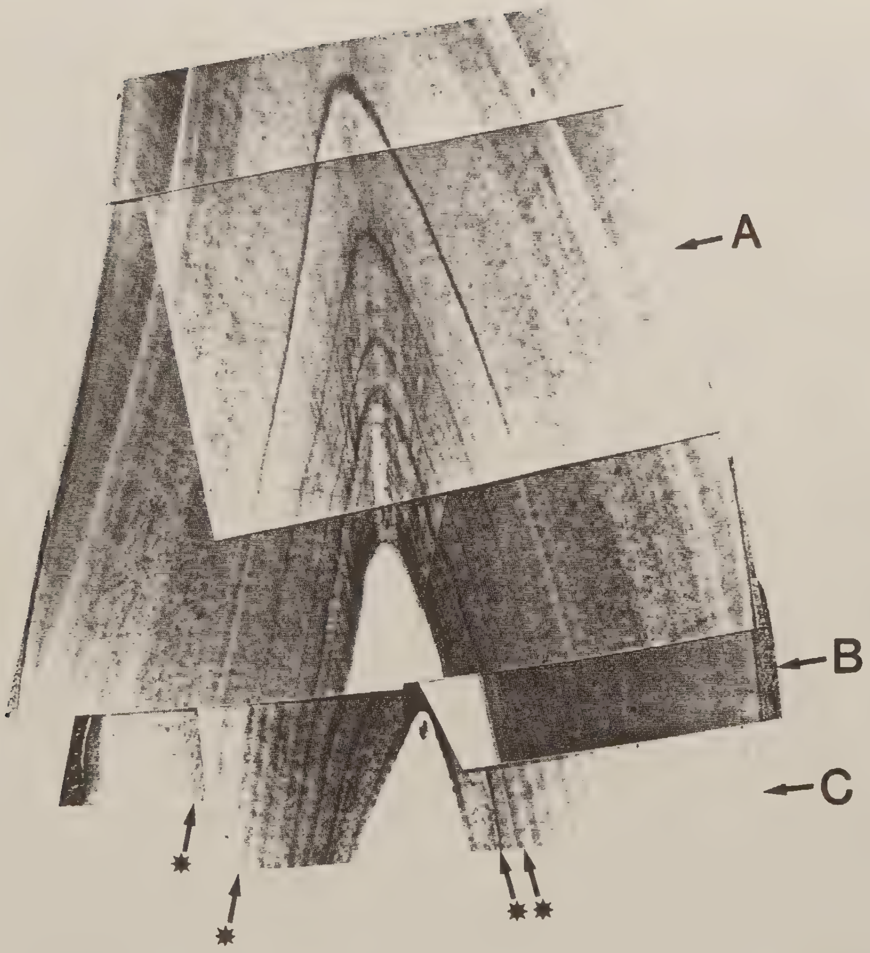

Fig. 8.4. Dentinal layering patterns of three individual spotted dolphins compared. Photographs of teeth from three specimens (A, B, C) are superimposed to show that a pattern common to all exists. B is the youngest, A the next youngest, and C the oldest. The three specimens were collected in different areas of the eastern central Pacific in different years. Although the patterns resemble one another closely, it is not difficult to locate individual differences (probably reflecting physiological differences), some of which have to do with intensity of some of the incremental layers (starred).

CALIBRATION

In early studies of the teeth of wild dolphins, there was no way to know for sure how long it took to lay down each similarly layered group of tissues, more recently termed growth layer groups, or GLGs (Perrin and Myrick 1980). Because of this initial uncertainty, tooth ages of dolphins were often stated in layer or GLG units, not in months or years. Before the full importance of thoroughly calibrating dental layers was realized, however, more than a few studies treated layer units as though layering rates had been measured. The lack of thorough calibration, as well as the subjectivity involved in selecting an "annual" layer or GLG, may account for some of the disparity in age-specific parameters given by different authors for different dolphin populations (Perrin and Reilly 1984).

One method used to calibrate the GLG deposition rate is to study the teeth of captive-born dolphins, because the ages are already known exactly. A count of GLGs in a single tooth from a dolphin of known age helps to verify the elapsed postnatal time they represent. Another method in use compares GLGs in teeth pulled from an animal in different seasons or years. A third approach is to mark the teeth of captive dolphins with tetracycline. Later, after the animals eventually die or when a tooth is removed from each live animal, elapsed time is compared with the number of GLGs formed after the tetracycline mark to estimate deposition rate.

A tooth from a captive-born dolphin of known age may show how many GLGs have been deposited since birth, but it gives no clue as to when a given GLG was formed or how long the process took: a deposition rate cannot be firmly established. A series of teeth extracted from an animal over time should provide a number of time periods within which the deposition of specific annual GLGs is defined with greater precision. But many teeth would have to be pulled over extended periods to determine deposition rates—a drawback to subject and experimenter alike.

Tetracycline marking, however, can be carried out repeatedly on a single animal to produce labels that are deliberately introduced weeks, months, or years apart. This permits examination and verification of deposition rates at almost any scale of detail.

Four features make tetracycline the GLG calibration tool of choice: (1) it combines immediately with the calcium incorporated into a newly forming incremental layer of dentine or cementum, (2) unabsorbed amounts of the drug are excreted within a few days after entry into the circulatory system, (3) when combined with the calcium in a layer viewed microscopically in ultraviolet light, tetracycline shows up as a fluorescent label among the layers in a tooth thin section, and (4) because it is an antibiotic, tetracycline causes no ill effects when introduced intramuscularly into a dolphin in low or moderate concentrations (30 to 75 mg/kg body weight, scaled to resting metabolic rate).

Of the three methods in use, multiple introductions of tetracycline over several years would seem most useful for determining deposition rates. Of course, the use of all methods together would be superior to any one of the three alone.

In 1979, I began a three-and-a-half-year experiment, assisted by staff members of Sea World, Inc., and Hubbs Marine Research Institute, to monitor the dentinal and cemental deposition rates in dolphin teeth. We used twelve bottlenose dolphins (*Tursiops truncatus*), including three captive-born animals and two control animals, maintained for public display by Sea World, Inc. Two of the wild-captured dolphins were from the California Pacific Coast and the remainder were from a population occupying coastal waters near Florida.

At the beginning of the experiment, we injected each animal with tetracycline and we extracted a tooth from each. (We used an extractor and an elevator after temporarily deadening the interalveolar nerve with a local anesthetic. The procedure is simple and apparently causes the animal little discomfort, and dolphins have plenty of teeth to spare.) About every three months thereafter we gave tetracycline to all but the control animals, and at approximately six-month intervals, we removed a tooth from all but the controls. In addition, sham events, in which animals were handled but did not undergo treatment or tooth removal, were conducted on the project animals at arbitrary intervals. At the end of the project (fall 1982), a tooth was taken from all animals (Myrick and Cornell 1990).

During the experiment, we kept weekly records of water temperature and salinity measurements, and we recorded weekly averages of types and amounts of food consumed. We also noted any changes in behavior, activity, and apparent health and any episode that might be stressful, such as unusual amounts of handling of an animal or transporting of any animals between Sea World parks (in Cleveland, Ohio; Orlando, Florida; and San Diego, California). In addition, we recorded body weight and length measurements at each labeling or extraction session.

In 1980, with the cooperation of colleagues at Sea Life Park, Waimanalo, Hawaii, I also conducted a GLG calibration study of captive Hawaiian spinner dolphins (*Stenella longirostris*), in two stages: (1) a retrospective phase, and (2) a direct monitoring phase. For the retrospective phase, we used teeth of four carcasses (including a captive-born specimen) and three live animals. All seven specimens had received numerous therapeutic doses of tetracycline at various times over periods of years during their captivity, and I thought it highly likely that each treatment had inadvertently labeled teeth of the recipient. (Fortunately, the labels

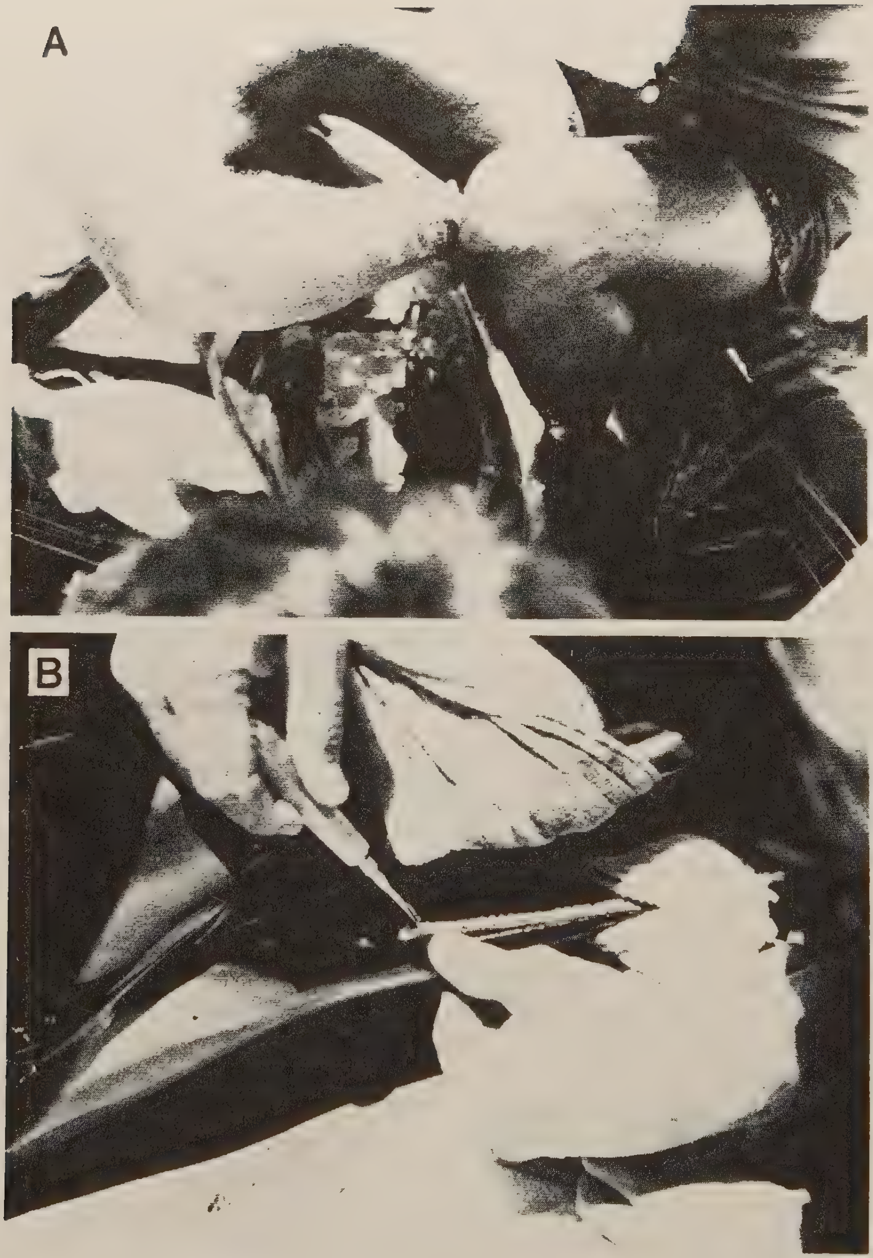

Fig. 8.5. Dental labeling and tooth extraction. A. Hawaiian spinner dolphin (*Stenella longirostris*) receiving tetracycline injection to introduce a label into the dental tissues for layer calibration studies. B. Removing a tooth from the anesthetized lower jaw.

had been introduced.) With labels identified to dates of past therapeutic treatments taken from records provided by Sea Life Park, we were able to document depositional rates from many years earlier.

In the direct monitoring phase of the Sea Life Park study, we extracted three teeth and gave three additional tetracycline injections, over a one-year period, to each of the three live captive animals to monitor dental tissue accumulation directly (Myrick et al. 1984; fig. 8.5). During the year, no environmental or behavioral records were systematically made.

Appropriately prepared, multiply labeled tooth thin sections from both the Sea World and Sea Life Park experiments were examined separately under plain and ultraviolet light. By tracing labels and layers on plastic overlays of ultraviolet- and plain-light photographs of each specimen, I was able to determine the position of each label within the layering pattern of each tooth. I matched almost every label to a treatment date by comparing the spacing, brightness, and thickness of each label in a tissue with the relative elapsed time between treatments and the length and dose strength of each treatment. With labels identified and series of units of layered tissue bracketed by dates, it was a simple step to identify, measure (in μm), and characterize repeating annual and subannual depositional patterns (fig. 8.6).

What made the two studies successful was the scrupulous manner in which the extensive medical records were maintained for each animal by Sea Life Park and Sea World staff members. Although the records were complete and virtually error-free, a certain amount of detective work had to be done to try to identify labels in a few specimens for which no corresponding dates of treatment were found. In the case of one of the captive-born bottlenose dolphins in the Sea World project, a narrow label occurred in the postnatal dentine a scant distance from the neonatal layer, but the animal had no corresponding treatment record. Since it was not usual for very young calves to be treated with antibiotics or to take solid food, I guessed that the dam who suckled the calf had been given tetracycline, which combined with her blood calcium and was imparted to the calf through her milk. An examination of the dam's records revealed that about one month after the calf was born, the dam was being treated with tetracycline (Myrick and Cornell 1990).

A more complicated mystery was encountered in the Hawaiian spinner study (Myrick et al. 1984). Teeth of the (deceased) captive-born dolphin contained numerous labels, but its records indicated that it had been treated with tetracycline on only three occasions during the three and three-fourths years that it lived (fig. 8.7). I found two faint closely spaced labels within the dentine formed in the first year of postnatal life (fig. 8.7A), which corresponded to records showing that the calf's dam was

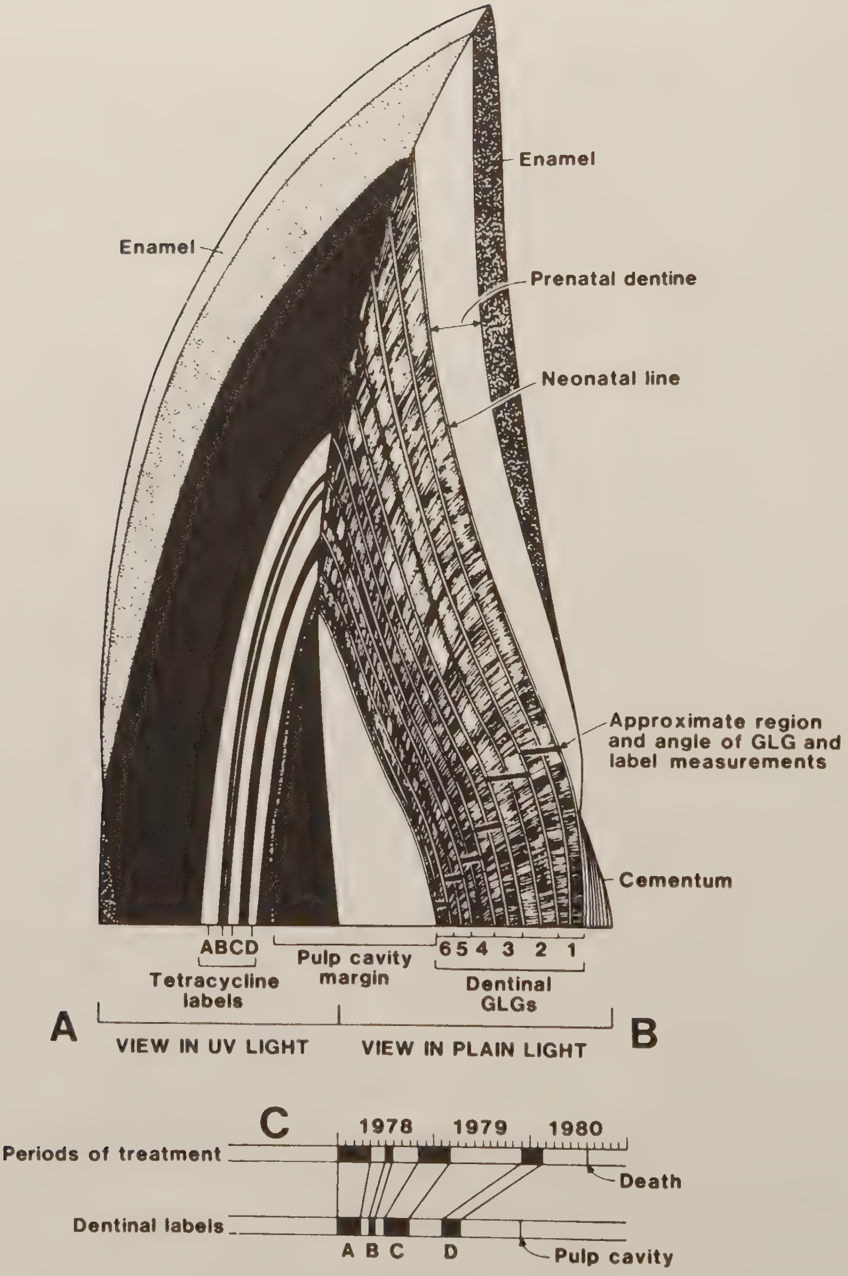
Enamel
Enamel
Prenatal dentine
Neonatal line
Approximate region and angle of GLG and label measurements
Cementum
ABCD
Tetracycline labels
Pulp cavity margin
6 5 4 3 2 1
Dentinal GLGs
A
VIEW IN UV LIGHT
VIEW IN PLAIN LIGHT
B
C
1978
1979
1980
Periods of treatment
Death
Dentinal labels
A B C D
Pulp cavity

Fig. 8.6. Line drawing of hypothetical dolphin tooth in thin section showing appearance of tetracycline labels, A, B, C, D, under UV light (A, left-hand side) and dentinal growth layer group (GLG) layering patterns under plain transmitted light (B, right-hand side). C illustrates method of identifying labels by comparing relative thickness and spacing of labels to duration of and elapsed time between treatments. (From Myrick et al. 1984.)

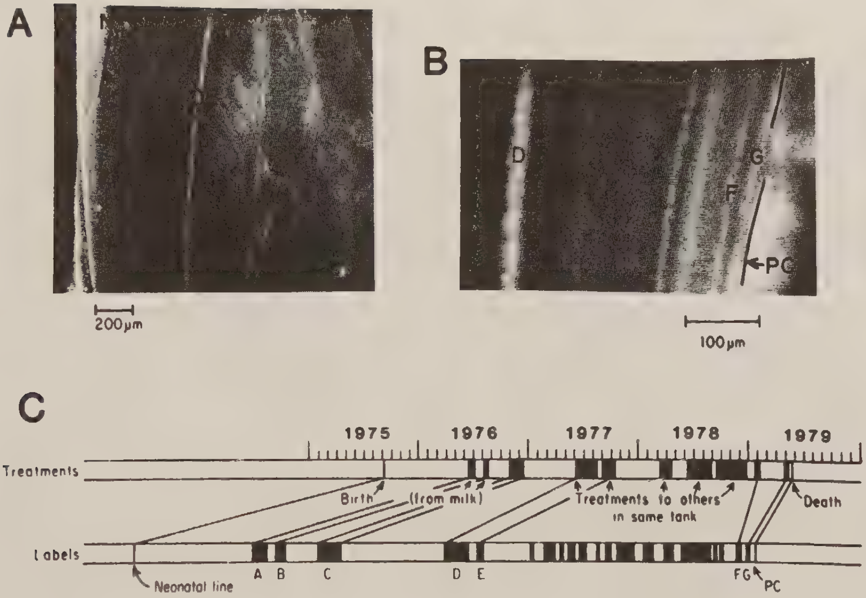

Fig. 8.7. A, B. Ultraviolet-light view of tetracycline labels in dentine of known-age Hawaiian spinner dolphin. C. Illustration of how labels were identified with intentional and unintentional introductions of tetracycline fluorophores. Labels A and B apparently were introduced when calf's dam was treated with tetracycline for two periods while the calf nursed. Labels received in 1977 and 1978 were introduced when the youngster stole and ate tetracycline-dosed smelt intended as treatment for other dolphins in the tank. (From Myrick et al. 1984.)

treated with tetracycline during two periods while she suckled the calf. (We proposed that a method of treatment might be developed using nursing as a vehicle to transmit certain medicines to sick calves in captivity without disturbing the calves or separating them from their dams (Myrick et al. 1984).

The mystery of the other undocumented labels in the teeth of the captive-born Hawaiian spinner dolphin solved itself when I matched the records of other dolphins that, at various times, had shared tanks with this young animal. Dolphins are usually treated with tetracycline by slipping the pills inside fish that are then given as food to the patients. As I discovered, many of this young animal's tank companions were being treated with tetracycline-dosed smelt. Interviews with a staff member confirmed that the young dolphin was very adept at stealing and eating fish intended for others and had been observed doing so with some frequency (fig. 8.7B,C).

MONTHLY LAYERS

Multiple labels introduced into the dentine only weeks or months apart showed repeatedly, in various specimens, that annual GLGs consist of thin layers that are deposited with lunar monthly regularity (Myrick et al. 1984). These results support observations made earlier suggesting that incremental layers of annual dentinal GLGs represent monthly records (Laws 1962; Kasuya 1977; Myrick 1979, 1980; Hohn 1980; fig. 8.8).

With the assumption that the dentinal recording device is keeping some sort of lunar monthly time, we may be able to develop a new tool that could furnish us with information about the dolphins in which lunar monthly layers are distinctly visible. A back-count of monthly layers might yield the year and month of birth of an individual if the date of its death is known.

Yearly peaks or other patterns in reproduction, including year-to-year changes in reproductive activity, should be detectable by monthly layer determinations of birth dates of specimens from a population sample

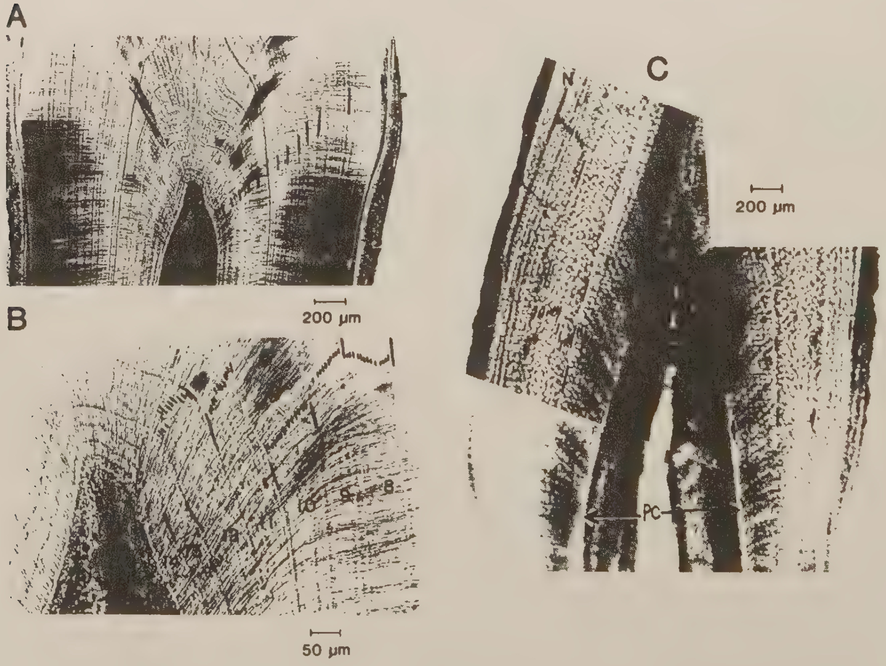

Fig. 8.8. Dentine of Hawaiian spinner dolphins showing apparent lunar monthly layers (fine marks) within the GLGs (heavy marks). A, B. Two magnifications of same specimen. C. Tooth of known-age dolphin. (From Myrick et al. 1984.)

(Myrick 1980, 1984*a*). If, for example, monthly layer counts for most of the specimens sampled from one population produced a significant birth peak in March and the gestation period was twelve months long, then serious perturbations of the population in the early spring might interfere with courting, breeding, and calving sufficiently to alter reproductive rates. Suppose another sample of the same hypothetical population is taken ten years after the initial sample and seven years after three successive years of strong El Niño conditions in the spring. Monthly layer counts from the new sample produce a broad birth peak at May-June-July. From this, a hypothesis might be formulated that the protracted change in the environment in the spring was connected with the shift in and broadening of the reproductive season.

Inferences might be made of the reproductive compatibility or isolation of two or more geographically contiguous populations from reproduction patterns generated from the counts (Myrick 1984*a*). If counts for the sample from one population produce a significant peak for spring and counts for the sample from another population produce a peak only for fall, a case for limited interbreeding between the two populations might be considered.

If the reproductive season of a population is limited to a short period, monthly layer counts might be used to estimate the approximate months of death in analyses of "die-offs" suspected of being connected with environmental changes (Myrick 1984*b*). Consider a hypothetical case in which several months after a huge oil spill, remains of many dolphins become washed up on nearby beaches. Morphometrics indicate that the specimens are from an offshore population whose calving season is in October and November. The oil spill is suspected of being connected with the large die-off of dolphins. Counts of monthly layers (from neonatal layer to pulp cavity) in teeth of the beach-cast specimens would give the number of lunar months from the beginning of November (the middle of the two-month peak calving season) until they died. In other words, counts would indicate the approximate month in which the animals died and whether deaths occurred at about the same time as the oil spill.

GENETICALLY BASED PATTERNS

Our calibration experiment with the bottlenose dolphins included detailed monitoring of food consumption, weekly average water temperature and salinity, and notation of handling, activity, and behavior. I examined dentinal and cemental layers that were deposited during periods of sudden fluctuations in some of these monitored conditions, for example, abrupt drops in water temperature, expecting to find corresponding alterations or interruptions in the regular layering patterns. Instead, comparisons showed that monitored exogenous changes had no perceptible effect on dentine deposition or layering pattern.

When I compared patterns of all the Sea World project specimens captured from the Florida coast, I found them to be very similar, especially in the annual thickness of dentine deposited at a specific age. I then compared the Florida pattern with the pattern exhibited in common by the two Pacific Coast captives in the project sample. In this comparison, I noted a sharp difference in age-specific GLG thicknesses between Florida and Pacific Coast specimens, even though they belonged to the same nominal species (*T. truncatus*). For example, Florida coast captives deposited dentinal GLGs in the first, second, and third years of life which were at least half again the thickness of those deposited by project specimens representing the Pacific Coast population. Such results are suggestive of a genetically determined dentinal depositional pattern, but the possibility exists that patterns and their differences could be an artifact, somehow, of the captive situation.

To consider the idea of genetically based patterns in greater detail, some colleagues and I compared annual GLG depositional patterns of Sea World captives from Florida waters with patterns in teeth taken from thirteen wild Florida coastal bottlenose dolphins captured and quickly released back into the wild (Myrick et al. 1985). Because they were from a population that had been the subject of extensive field studies for many years, the wild animals were individually identifiable and had been monitored from year to year, so that they were either of known age or known minimum age.

In the captive/wild pattern study, we used the age-specific dentinal GLG pattern (developed from studies of Sea World Florida coast captives) to estimate the tooth ages of the wild dolphins. The ages of the wild dolphins were already documented by the field studies, but they were unknown to me at the time I made the tooth age estimates. We wanted to determine whether wild and captive animals from the same population had similar depositional rates and patterns. An answer to this question would also resolve whether or not the wild pattern was measurably altered by conditions of captivity. Results showed that the age estimates made with the captive pattern of GLG thicknesses as a guide were very close to the known ages of the wild dolphins (Myrick et al. 1985). These results and the results of an earlier study in which I found layering and thickness patterns to be nearly identical in spotted dolphins and Hawaiian spinner dolphins (*Stenella attenuata* and *S. longirostris;* fig. 8.9) are evidence that at least some of the pattern is genetically determined (Myrick et al. 1983).

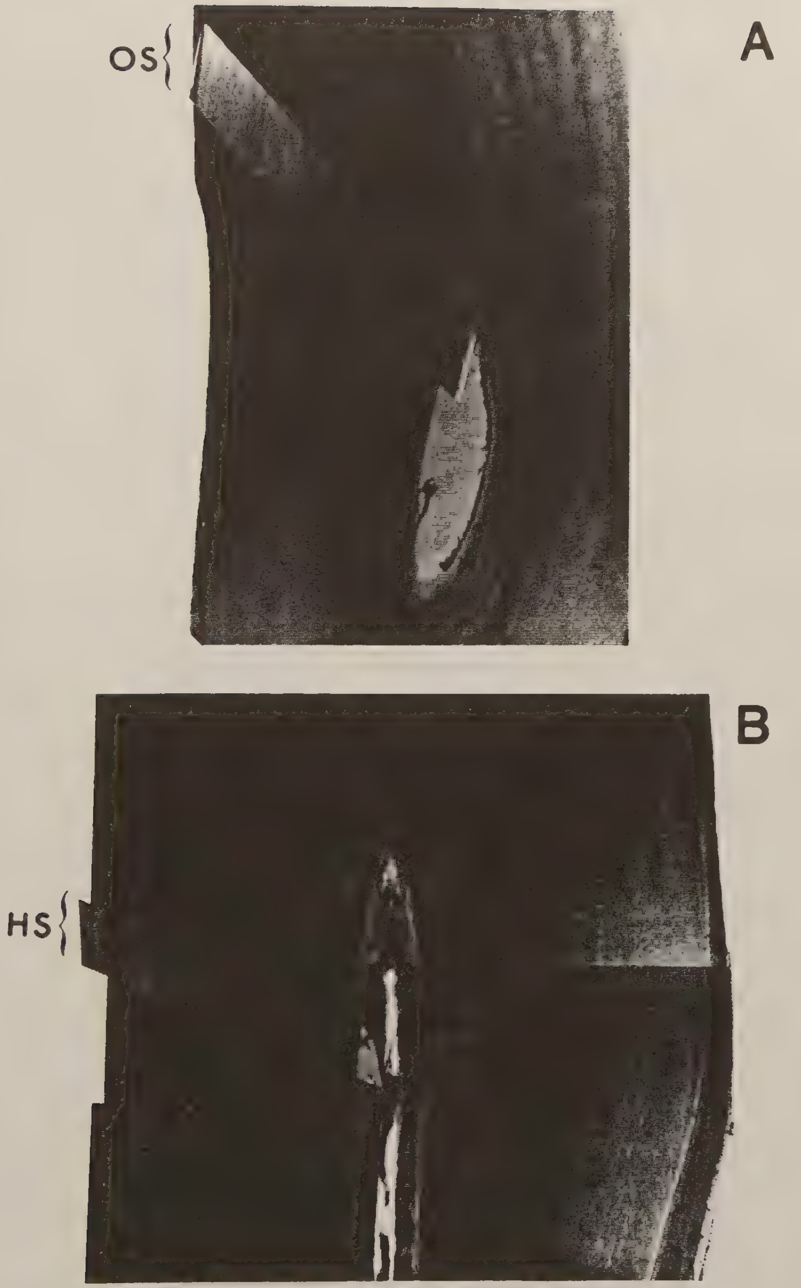

Fig. 8.9. Swatches of dentine from a specimen of one species of dolphin imposed on the dentinal pattern of a specimen of a different species to show pattern similarities and dissimilarities. A. Offshore spotted dolphin (OS), *Stenella attenuata,* swatch on Hawaiian spinner dolphin, *Stenella longirostris,* tooth. B. Hawaiian spinner dolphin swatch (HS) on offshore spotted dolphin tooth. (From Myrick et al. 1983.)

If adequate criteria can be established to define unique genus-, species-, or subspecies-specific patterns, future studies might use patterns to determine genetic closeness (fig. 8.4), perhaps even the degree of interbreeding, of contiguous or adjacent dolphin populations. The degree of physical and genetic separation of stocks belonging to the same species is of vital interest in fisheries management. In the case of the ETP purse seine fishery, for example, it is sometimes difficult to distinguish between two stocks of spinner dolphins (*Stenella longirostris*) affected by fishing operations because of the rather high overlap in external identifying characteristics (Perrin et al. 1985, Anon. 1986).

INDIVIDUAL VARIABILITY

It is not difficult to detect individual variability within what I suspect are species-specific patterns (fig. 8.4). However, based on calibration studies previously described, it must be concluded that exogenous factors that we monitored probably do not cause measurable pattern variability. I found no pattern variation associated with removing an animal from the water, changing the diet from pure fish to mixed fish and squid, or environmental changes, such as seasonal water temperature fluctuations or transporting animals to locations differing in latitude by up to 13 degrees (Orlando to Cleveland) (Myrick and Cornell 1990). An animal in one of the calibration studies accidentally leaped out of its tank. It remained out of the water, on the ground, perhaps for hours before it was discovered and returned to the tank, apparently uninjured. This unpredictable accident provided us with an excellent opportunity to test whether an "instantaneous," presumably stressful situation causes dentinal pattern variability. Later, when I examined the dentine formed during the period encompassing the accident, I could discern no changes in the normal pattern.

Variation within dentinal layering patterns is more conspicuous and more frequent in female dolphins than in males. In decalcified and stained thin sections of teeth, much of the variability exists as thin, intensely stained layers that are intermittently distributed in the dentine and that stand out rather starkly against the comparatively muted normal pattern of differentially stained layers of the GLGs.

In a study of the dentinal patterns in *Stenella* spp. (Klevezal' and Myrick 1984), we found that most of these strongly contrasting layers (SCLs) occur in females in dentine formed after attainment of sexual maturity. It seemed likely to us that SCLs could represent dentinal calcium fluctuations connected with reproductive cycles of the females—possibly calving events. To test this idea, Klevezal' and I first looked at thin sections of tetracycline-labeled teeth from a captive female Hawaiian spinner dolphin that had given birth to a calf while in captivity. This animal was one of the seven specimens used in the study to calibrate dental layers in teeth of Hawaiian spinner dolphins (Myrick et al. 1984). We then studied tooth thin sections of seventy-five sexually mature female spotted dolphins selected from a larger, random sample used for age-specific reproduction studies (Myrick et al. 1986). Sexual maturity of a female was determined by the presence of at least one ruptured Graafian follicle (corpus luteum) or a scar from such a rupture (corpus albicans) on either ovary, indicating that the animal had ovulated at least once.

The Hawaiian spinner dolphin had been in captivity for about ten months when she delivered a calf; the calf survived for only three days. One month after parturition, the dam was started on a therapeutic treatment of tetracycline that lasted more than one month. This treatment produced a dentinal label identified as Label B in the teeth of this animal (Myrick et al. 1984; fig. 8.10). To locate Label B for the SCL study, we had to use untreated thin sections (because treating teeth involves decalcification, which destroys the labels). To look for any SCLs near the position of Label B, we had to use decalcified and stained thin sections (because SCLs are narrow, dark-stained layers). After only a little searching of the decalcified and stained dentine, we identified an SCL in about the same position as Label B in the untreated thin sections (fig. 8.11). This reinforced the idea that SCLs were connected with some part of the female reproduction cycle. But, what part? Did SCLs represent pregnancy, parturition, early lactation, or all or none of the above?

To limit the number of possibilities, we began the other part of the study using teeth from the seventy-five female spotted dolphins. This exercise was different from the search for the SCL in the Hawaiian spinner dolphin tooth, in that we independently identified, counted, and noted the position of SCLs for each specimen without knowing anything about the reproductive condition of the specimen in advance (except that each female was sexually mature).

We erected five hypotheses directed at the question of which condition (if any)—pregnancy, ovulation, parturition, lactation, or parturition and lactation—was most frequently associated with the presence of an SCL. The following reasoning was used in reaching our conclusions:

1. If the layers have no specific connection with reproduction, then they are just as likely to occur in reproductively inactive females as in reproductively active females. [They did not.]
2. If the layers represent ovulations, then they should be exactly equal in number to the total count of ovarian corpora (because corpora, once formed, probably never disappear) (Perrin and Donovan 1984).

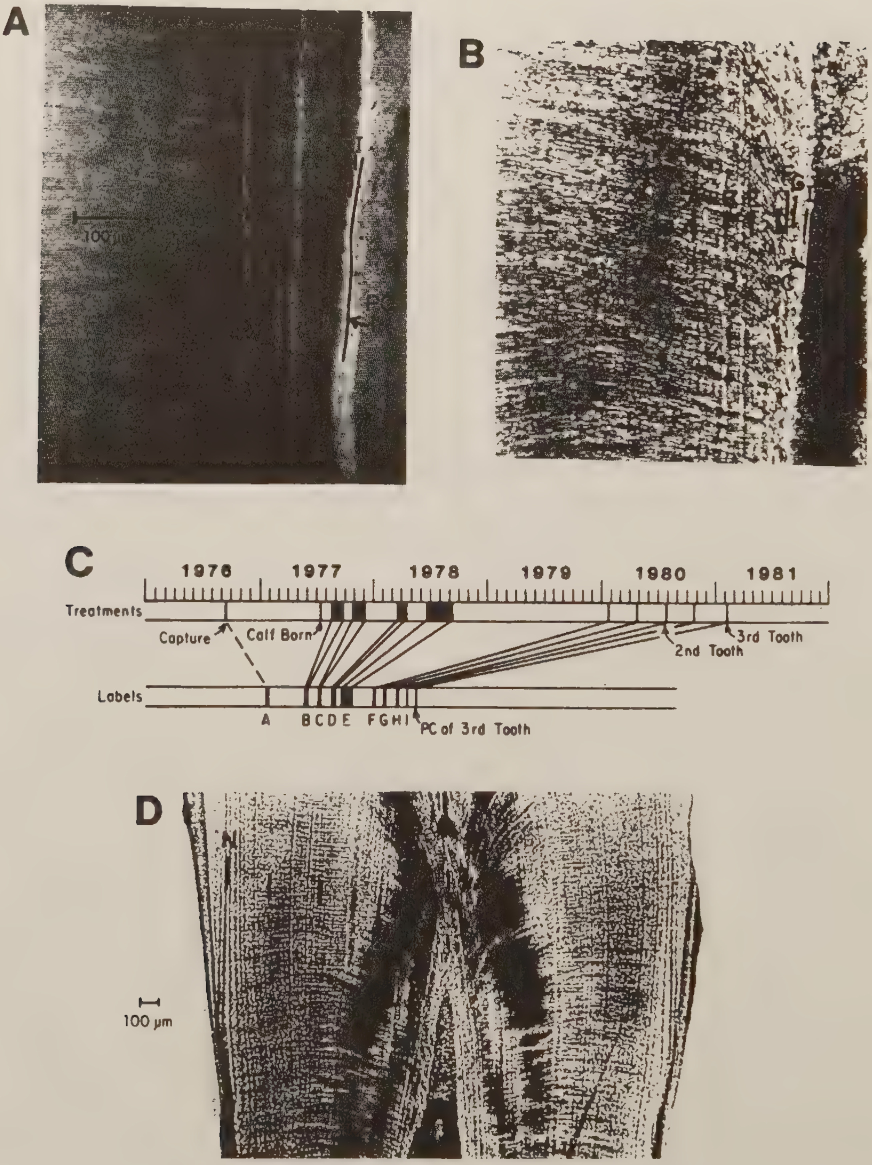
A
100 µm
B
C
1976
1977
1978
1979
1980
1981
Treatments
Capture
Calf Born
2nd Tooth
3rd Tooth
Labels
A
B C D E
F G H I
PC of 3rd Tooth
D
100 µm

Fig. 8.10. Tooth labels, layers, and matching of labels with treatment dates of female Hawaiian spinner dolphin that gave birth to a calf in captivity. A. Labels are lettered A-I. Label B was introduced one month after the female gave birth. PC = pulp-cavity margin. B. Labels are located in layered tissues by marking plastic overlays of UV photos and plain-light photos. C. Labels matched to treatment dates using label spacing and treatment duration. D. Gross view of layering pattern across entire tooth. (From Myrick et al. 1984.)

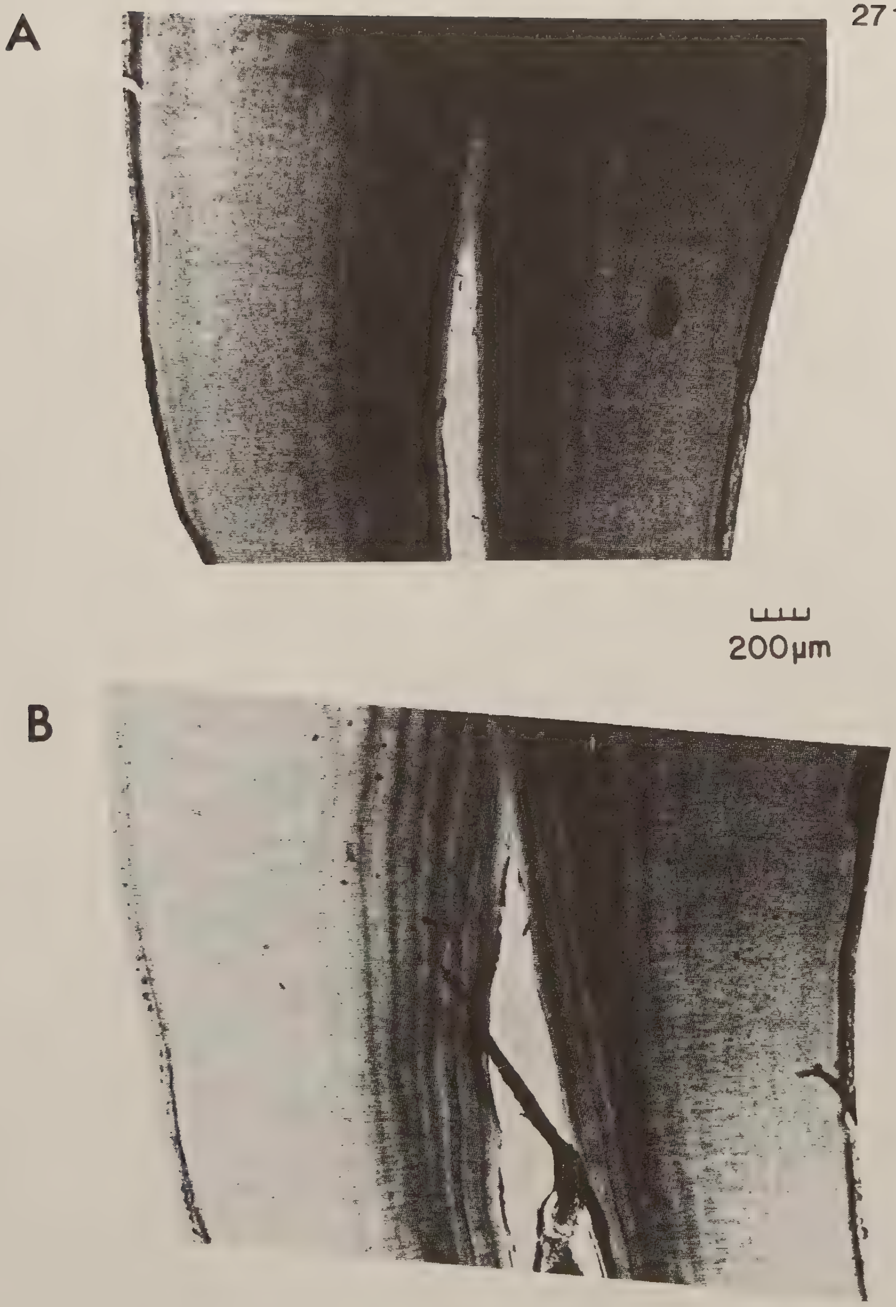

Fig. 8.11. A, B. Photographs of two decalcified and stained thin-sectioned teeth from female Hawaiian spinner dolphin that gave birth in captivity. A strongly contrasting layer (SCL), indicated by arrow, is near the position of a tetracycline label introduced one month after the female's calf was born. (From Klevezal' and Myrick 1984.)

Table 8.1. *Tooth Layering and Reproductive Condition in Female Spotted Dolphins*

Hypotheses— Formation of SCL Associated with:	*Tests of Coincidence*	*Total Number of Specimens*	*Coincidence*		*Noncoincidence*		*Result of Test*
			NUMBER OF SPECIMENS	PERCENT	NUMBER OF SPECIMENS	PERCENT	
1. Ovulation	1a. SCL count = CAs + CLs	75	10	13	65	87	Negative
a. all ovulations b. all but most recent fertilized ovulation	1b. SCL count = CAs + CLs excluding CLs of pregnancy	75	17	22	58	78	Negative
2. Pregnancy	2a. In all pregnant females, SCL in last GLG	30	1	3	28	97	Negative
3. Parturition or lactation	3a. SCL count ≤ CAs + CLs excluding any CLs of pregnancy	75	70	93	5	7	Positive
	3b. In all pregnant females, SCL count < CAs + CLs of pregnancy	75	70	93	5	7	Positive
4. Lactation only	4a. In all lactating females, SCL in last GLG without a space between SCL and pulp cavity	40	0	0	40	100	Negative
5. Parturition only	5a. In all lactating females, at least one SCL within the last two GLGs	40	35	88	5	12	Positive

Note: This table compares the percent coincidence tests of five hypotheses of relationships between SCLs and reproductive condition in female spotted dolphins (*Stenella attenuata*). SCL: strongly contrasting layers; GLG: growth layer group; CA: corpus albicans; CL: corpus lutem. (Modified from Kevezal' and Myrick 1984.)

3. If the layers represent pregnancies, then in nonpregnant females, they should be equal to or less than the total count of ovarian corpora (because not all ovulations may result in pregnancy). Furthermore, in all pregnant females, an SCL should be present within the last-formed dentinal GLG (because the female was pregnant at death).
4. If the layers represent lactation, then SCLs should be equal to or less than the total count of ovarian corpora (because lactation is preceded by a pregnancy and not all ovulations may result in pregnancies). Furthermore, in all lactating females, an SCL should be present within the last-formed dentinal GLG without a space between it and the edge of the pulp cavity (because the female was lactating when killed).
5. If the layers represent parturition only, then the first point in #4 should be true. Furthermore, in all lactating females, an SCL should be present within the two last-formed GLGs (because nursing may continue for more than a year after parturition) (Perrin and Reilly 1984).

The percent coincidence tests we used showed a consistently strong (83–93%) association of layers with parturition exclusive of lactation (table 8.1). The tests excluded the high likelihood of SCLs as indicators of any other condition that we considered.

Since that study, I have had the opportunity to examine the teeth of three long-lived, captive female bottlenose dolphins with extensive reproductive and calving histories. Two had each given birth to three calves; the other, to one calf. I found a parturition layer in the dentine formed during the date recorded for each calving event (fig. 8.12). I also noted similar spacing of anomalous layers in the cementum of these specimens.

Reliable criteria for detecting SCLs that indicate parturition would be extremely useful in managing dolphin populations. In the case of the dolphins associated with the yellowfin tuna purse seine fishery, evaluation of the fishery's historical impact on the size and health of the dolphin populations has been a major problem. The dolphins became directly affected by the fishery in 1959 when the fishing method changed from bait fishing to purse seining. From that time through the 1960s and into the early 1970s, dolphin fishing mortality is estimated to have reached between 100,000 to 400,000 animals annually (Smith 1983). The impact assessment problem exists because (1) there are no firm estimates of pre-1959 population levels of dolphins (numbers of individuals), (2) the dolphin populations are presumed to have undergone changes in reproductive rates as a density-dependent response to the substantial fishing mortalities, and (3) almost no mortality samples were collected before 1972 (long after the populations are presumed to have responded to the effects

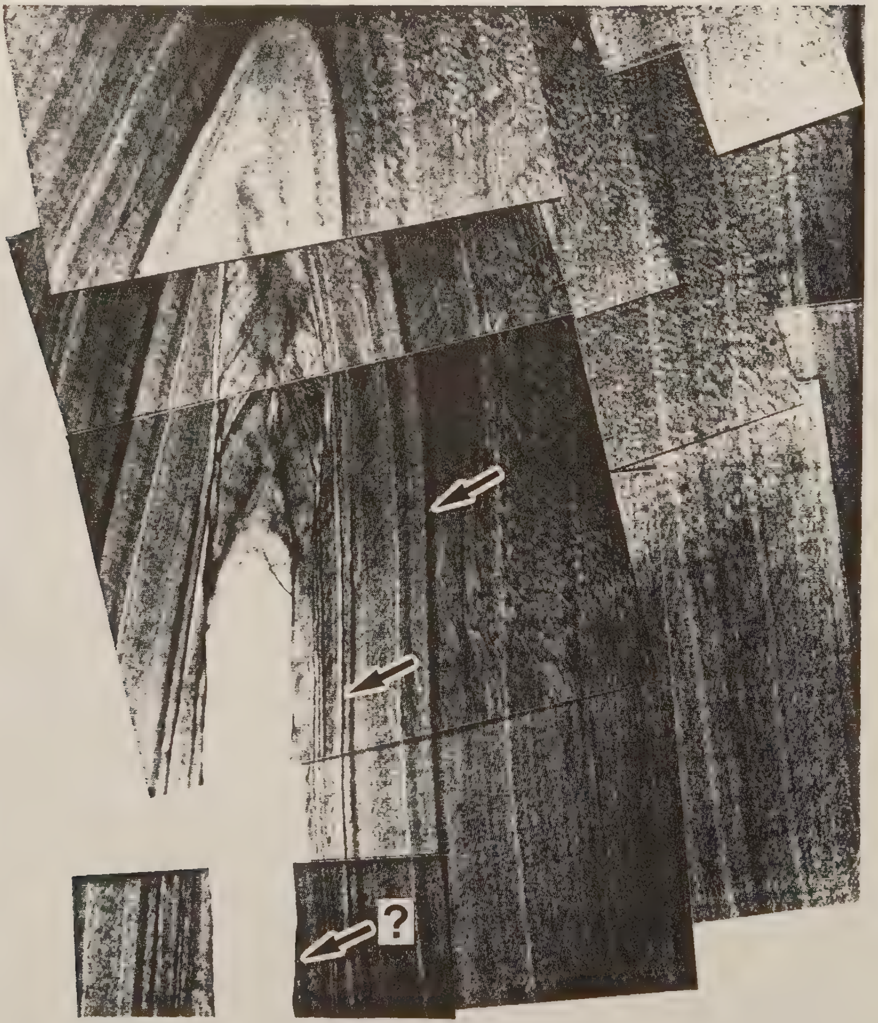

Fig. 8.12. Highly magnified section of decalcified and stained tooth from a female bottlenose dolphin that gave birth to three calves in captivity. Two strongly contrasting layers, SCLs (arrows), occur in the regularly layered dentine, a third may be next to the pulp-cavity margin (the female died not long after giving birth to the third calf).

of the high kills). In short, virtually no information exists concerning the dolphins before the 1970s.

If SCL definitions can be refined for ready identification, possibly they could be used to interpret the reproductive histories, including per-capita calf production and calving frequency, of sexually mature females from their dentinal and cemental patterns. The years of heavy kill did not take place before 1959 (13 years before sampling started), and the average age at sexual maturity for females is between 6 and 11 years old (depending on the population). These two facts indicate that tooth samples of females between 20 and 35 years old collected in 1973, 1974, and 1975 should contain SCLs that were formed well before the introduction of purse seining. If such specimens exist in sufficient number, they could be useful in the estimation of reproductive rates that occurred before the impact of purse seine fishing. In addition, counts and spacing of SCLs in those and younger specimens might help fill the data gap concerning any changing rates during the heavy-kill period (1960–1975). This possibility has not yet been examined in any detail.

SUMMARY

Results from research that I initially conducted to develop more accurate age determination methods show that layers in dental tissues have a much greater potential as tools for biological inquiry than merely servicing the need for age estimates. Now that layering patterns in various species are being calibrated with time, it soon may be possible to use monthly layers to estimate peak reproductive seasons for a population and, thereby, to measure the degree of reproductive compatibility between adjacent populations.

Several of our studies have shown that local exogenous fluctuations do not perceptibly alter the genetically based dentinal layering patterns. This permits consideration of the use of dentinal patterns to estimate genetic closeness of sampled populations at the genus, species, and even perhaps at the subspecies level.

Recognition of the existence of genetic patterns has facilitated the identification of individual variation within the patterns. Because external factors do not seem to affect the patterns, variation must reflect, to a large extent, certain individual physiological changes. Parturition layers in sexually mature females seem to be a likely example of this. These layers are a prime candidate for development as a tool for population management because they may provide a record of the complete calving history of a female. In addition, other variations in the dental patterns are known to exist in both male and female delphinids. There is little doubt that they reflect other physiological events or biological cycles yet to be identified. Extensive study and experimentation will be needed to determine if such potential tools can be fully developed for practical use.

Despite the very difficult task of trying to study such secretive animals as dolphins, techniques are being developed and improved to address some of our most important questions concerning delphinid biology. In the 1950s, researchers were developing a tool for estimating a dolphin's age. Since then, the method has been used to help provide answers to questions about the reproductive health and future growth of dolphin populations. Results of the calibration studies that I have described should add greater firmness to some of those answers, but it is becoming increasingly clear that dental recording devices of dolphins have been underutilized as potential sources of biological information.

When we realize that the recordings themselves are chronological histories written in the biochemical language of the animals' own physiology, we are prompted to search for a Rosetta stone that will allow us to translate these histories. By learning what physiological conditions cause the recorded features, we can then use the features to interpret past conditions, as we are beginning to do with parturition layers. Perhaps, eventual interpretation of large parts of an individual's physiological history may be possible (see, for example, Myrick 1988).

After decades of work to understand the natural and human-caused environmental effects on tree growth, dendrologists are now able to determine much of the historical growth physiology of trees from details of their annuli. With dolphins, the problem differs only in our limited ability to monitor their wild environment and their physiological responses to it closely enough. Until that ability is achieved, we must settle for remote and retrospective monitoring to answer our questions about the dolphin populations. No doubt, some of these interim answers will come from layers in the teeth.

REFERENCES

Anon. 1986. A guide to shipboard identification of spinner and spotted dolphin schools (genus *Stenella*) in the eastern and central tropical Pacific Ocean. NMFS, SWFC Amin. Rpt. LJ-86-30. 23 pp.

Boyde, A. 1980 (1981). Histological studies of dental tissues of odontocetes. In: Age determination of toothed whales and sirenians, ed. W. F. Perrin and A. C. Myrick, Jr. Rep. Int. Whal. Comm. Spec. Issue 3. 65–87.

Hammond, P. S., and K. T. Tsai. 1983. Dolphin mortality incidental to purse-seining for tunas in the eastern Pacific Ocean, 1979–1981. Rep. Int. Whal. Comm. 33:589–597.

Hohn, A. A. 1980 (1981). Analysis of growth layers in teeth of *Tursiops truncatus*, using light microscopy, microradiography, and SEM. In:

Age determination of toothed whales and sirenians, ed. W. F. Perrin and A. C. Myrick, Jr. Rep. Int. Whal. Comm. Spec. Issue 3. 155–160.

Kasuya, T. 1977. Age determination and growth of Baird's beaked whale with a comment on the fetal growth rate. Sci. Rept. Whales Res. Inst. Tokyo 29 : 1–20.

Klevezal', G. A., and A. C. Myrick, Jr. 1984. Marks in tooth dentine of female dolphins (genus *Stenella*) as indicators of parturition. J. Mamm. 65(1) : 103–110.

Laws, R. M. 1962. Age determination of pinnipeds with special reference to growth layer in the teeth. Saugetier. Mitt. 27(3) : 129–146.

Myrick, A. C., Jr. 1979. Variation, taphonomy, and adaptation of the Rhabdosteidae (=Eurhinodelphidae) (Odontoceti, Mammalia) from the Calvert formation of Maryland and Virginia. Ph.D. dissertation, Univ. of California, Los Angeles. 411 pp. (Avail. Univ. Microfilms Intl.)

———. 1980 (1981). Examination of layered tissues of odontocetes for age determination using polarized light microscopy. In: Age determination of toothed whales and sirenians, ed. W. F. Perrin and A. C. Myrick, Jr. Rept. Int. Whal. Comm. Spec. Issue 3. 95–97.

———. 1984*a*. Reproductive seasonality in multi-herd groups of northern offshore spotted dolphins, *Stenella attenuata*, and age-related reproductive parameters for females. (Abstract) In: Reproduction in whales, dolphins and porpoises, ed. W. F. Perrin, R. L. Brownell, Jr. and D. P. DeMaster. Rep. Int. Whal. Comm. Spec. Issue 6. 480.

———. 1984*b*. Time significance of layering in some mammalian hard tissues and its application in population studies. Acta. Zool. Fennica 171 : 217–220.

———. 1988. Is tissue resorption and replacement in permanent teeth of mammals caused by stress-induced hypocalcemia? In: The biological mechanisms of tooth eruption and root resorption, ed. Z. Davidovitch. EBSCO Media, Birmingham. 379–389.

Myrick, A. C., Jr., and L. H. Cornell. 1990. Calibrating dental layers in captive bottlenose dolphins, *Tursiops truncatus*, from serial tetracycline labels and tooth extractions. In: The bottlenose dolphin, *Tursiops* spp., ed. S. Leatherwood and R. Reeves. Orlando: Academic Press.

Myrick, A. C., Jr., A. A. Hohn, J. Barlow, and P. A. Sloan. 1986. Reproductive biology of female spotted dolphins, *Stenella attenuata*, from the eastern tropical Pacific. Fish. Bull. 84(2) : 247–259.

Myrick, A. C., Jr., A. A. Hohn, R. S. Wells, M. D. Scott, and A. B. Irvine. 1985. Dentinal growth layer similarities in captive and wild known-age bottlenose dolphins, *Tursiops truncatus*. Proc. Abstracts, Fourth Intl. Theriological Congress, Edmonton, Alberta. Aug. 13–20, 1985.

Myrick, A. C., Jr., A. A. Hohn, P. A. Sloan, M. Kimura, and D. P. Stanley. 1983. Estimating age of spotted and spinner dolphins (*Stenella attenuata* and *Stenella longirostris*) from teeth. NOAA-TM-NMFS-SWFC-30. 17 pp.

Myrick, A. C., Jr., E. W. Shallenberger, I. Kang, and D. B. MacKay. 1984. Calibration of dental layers in seven captive Hawaiian spinner dolphins, *Stenella longirostris*, based on tetracycline labeling. Fish. Bull. 82(1):207–225.

Nishiwaki, M., and T. Yagi. 1953. On the age and the growth of teeth in a dolphin, (*Prodelphinus caeruleo-albus*). I. Sci. Rept. Whales Res. Inst. Tokyo 8:133–146.

Perrin, W. F. 1969. Using porpoise to catch tuna. World Fishing 18(6):42–45.

———. 1972. Color patterns of spinner porpoises (*Stenella* cf. *S. longirostris*) of the eastern Pacific and Hawaii, with comments on delphinid pigmentation. Fish. Bull. U.S. 70(3):983–1003.

———. 1975. Variation of spotted and spinner porpoise (genus *Stenella*) in the eastern tropical Pacific and Hawaii. Bull. Scripps Inst. Oceanog. (Univ. Calif. Press), vol. 21. 206 pp.

Perrin, W. F., and G. P. Donovan (eds.). 1984. Report of the workshop. In: Reproduction in whales, dolphins, and porpoises, ed. W. F. Perrin, R. L. Brownell, Jr., and D. P. DeMaster. Rept. Int. Whal. Comm. Spec. Issue 6. 1–24.

Perrin, W. F., and A. C. Myrick, Jr. (eds.). 1980 (1981). Age determination of toothed whales and sirenians. Rept. Int. Whal. Comm. Spec. Issue 3. 229 pp.

Perrin, W. F., and S. B. Reilly. 1984. Reproductive parameters of dolphins and small whales of the family Delphinidae. In: Reproduction in whales, dolphins, and porpoises, ed. W. F. Perrin, R. L. Brownell, Jr., and D. P. DeMaster. Rept. Int. Whal. Comm. Spec. Issue 6. 97–133.

Perrin, W. F., M. D. Scott, G. J. Walker, and V. L. Cass. 1985. Review of geographical stocks of tropical dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern tropical Pacific. NOAA Tech. Memo. NMFS-SWFC 28, 28 pp.

Peyer, B. 1968. Comparative odontology. Trans. and ed. R. Zangerl. Chicago: Univ. of Chicago Press. 347 pp. + 96 pls.

Scheffer, V. B., and A. C. Myrick, Jr. 1980 (1981). A review of studies to 1970 of growth layers in the teeth of marine mammals. In: Age determination of toothed whales and sirenians, ed. W. F. Perrin and A. C. Myrick, Jr. Rept. Int. Whal. Comm. Spec. Issue 3. 51–63.

Scott, J. H., and N. B. B. Symons. 1964. Introduction to dental anatomy. 4th ed. Edinburgh: E. & S. Livingstone Ltd., 406 pp.

Smith, T. 1983. Changes in size of three dolphin populations (*Stenella* spp.) in the eastern tropical Pacific. Fish. Bull. U.S. 81(1): 1–13.

Walker, E. P. 1968. Mammals of the world. 2d ed., revis. J. Paradiso. Baltimore: Johns Hopkins Univ. Press.

Age, Growth, and Potential Yield for Shortbelly Rockfish *Sebastes jordani*

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Abstract.– Shortbelly rockfish *Sebastes jordani* is an abundant species that could support a large commercial fishery off central California. Prior studies of shortbelly rockfish growth were based on age data obtained from scales or whole otoliths. We show that broken and burnt otoliths provide reliable ages that are substantially different than those derived from previous methods. This new information was used to update estimates of the von Bertalanffy growth curve parameters, the natural mortality rate, and potential yield. We found that shortbelly rockfish live for up to 22 years. Males grew more slowly and reached a smaller maximum size than females. Estimates of natural mortality from three predictive models ranged from 0.212 to 0.378 for males and 0.203 to 0.437 for females. Assuming M is 0.20–0.35 and using biomass estimates from hydroacoustic surveys, we estimated that potential yield in the Ascension Canyon–Farallon Islands area ranges from 13,400 to 23,500 metric tons.

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Shortbelly rockfish *Sebastes jordani* is an abundant species in California waters. In midwater trawl surveys of juvenile rockfish conducted off central California, shortbelly rockfish were far more abundant than any other rockfish species (Wyllie Echeverria et al. 1990). The biomass of shortbelly rockfish in the Ascension Canyon–Farallon Islands area was estimated from hydroacoustic studies (E. Nunnely, NMFS Alaska Fish. Sci. Cent., Seattle, WA 98115-0070, pers. commun., Jan. 1989) to be 295,000 metric tons (t) in 1977 and 152,700 t in 1980. These estimates are one to two times the estimated coastwide virgin biomass for widow rockfish *S. entomelas* (Lenarz and Hightower 1988), a species that supports a significant commercial fishery. Currently, there is no commercial or sport fishery for shortbelly rockfish, but interest in surimi production or a new method of bone softening of whole fish (Okada et al. 1988), combined with their high abundance, could lead to the development of a substantial commercial fishery. If a commercial fishery does develop, it will be important to have accurate life-history information for management purposes.

Previous studies of shortbelly rockfish life-history characteristics have been based on age data from scales (maximum age 10 years, Phillips 1964) or whole otoliths (maximum age 12 years, Lenarz 1980). However, studies of other rockfish species (Six and Horton 1977, Beamish 1979, Kimura et al. 1979, Chilton and Beamish 1982, Boehlert and Yoklavich 1984, Stanley 1986, Leaman and Nagtegaal 1987) have shown that ages obtained from those structures tend to be underestimates, and that broken and burnt or sectioned otoliths are a more reliable method for determining fish age. W. Lenarz (Tiburon Lab., NMFS Southwest Fish. Sci. Cent., Tiburon, CA 94920, pers. commun., Jan. 1989) indicated that surface ageing of shortbelly rockfish otoliths was difficult and felt that the ages could have been greater than reported. For that reason, the objective of this study was to update the estimates of age, growth, and potential yield of shortbelly rockfish, based on examination of broken and burnt otoliths.

Materials and methods

Adult shortbelly rockfish were captured occasionally in 1983–88 midwater trawl surveys designed to monitor the abundance of juvenile

Table 1
Number of trawl tows containing adult shortbelly rockfish by area and year. Numbers in parentheses indicate total number of fish in the samples.

Region	1980	1981	1982	1983	1986	1988
Cape Blanco to Newport, OR	2 (175)	2 (100)		3 (130)		
Point Arena	1 (54)	1 (18)				
Farallon Islands		1 (49)			1 (107)	
Pescadero	1 (108)	2 (10)				2 (60)
Ascension Canyon	6 (423)	3 (147)	3 (152)	1 (126)	2 (91)	2 (101)
Monterey						2 (97)
Point Sur		13 (630)				
Total	10 (760)	21 (954)	3 (152)	4 (256)	3 (198)	6 (258)

rockfish (Wyllie Echeverria et al. 1990). Samples were also obtained from a 1980 bottom-trawl survey of demersal adult rockfish (Gunderson and Sample 1980), and a 1981 fishery development survey using a midwater trawl (Kato 1981). The cod-end mesh size for these surveys ranged from 0.4 to 1.5 inches, and fish ages 1 and older were vulnerable to the gear. Otoliths were collected from 2238 fish from 48 tows at various locations along the northern California–central Oregon coast (Table 1). Sagittal otoliths were removed, cleaned, and either stored dry or in ethanol until they could be examined.

Following Kimura et al. (1979) and Lenarz (1987), we examined the edges of broken and burnt otoliths collected from all months to determine whether marks formed on an annual basis. We attempted to get at least 100 fish per month (pooled over years); however, sample sizes were less than 100 for February, August, September, October, and December (Fig. 1). The broken and burned otoliths were examined without knowledge of sex, length, or date of capture. A dark burned edge was classified as winter growth; otherwise, the edge type was classified as summer growth. A few otoliths that appeared to be from older fish, for which edge type could not be identified clearly, were omitted from the study. Percent frequency of summer growth was plotted against month to examine periodicity in the formation of marks.

We used between- and within-reader comparisons to evaluate the consistency of broken and burnt otolith readings. To evaluate between-reader agreement, two readers independently examined a random subsample of 200 otoliths. To evaluate within-reader agreement, a random subsample of 200 otoliths was read twice, independently, by one reader. To compare ages obtained by otolith surface versus broken and burnt otoliths, one reader obtained ages for a random subsample of 200 otoliths, first from the surface and then independently from the broken and burnt halves.

We used the von Bertalanffy growth equation (Ricker 1975) to relate length and age:

$$L_t = L_\infty (1 - e^{(-k(t-t_0))})$$

where L_t = total length (mm) at age t,
L_∞ = estimate of average maximum length attained,
k = growth completion rate,
t_0 = theoretical age when fish is length 0.

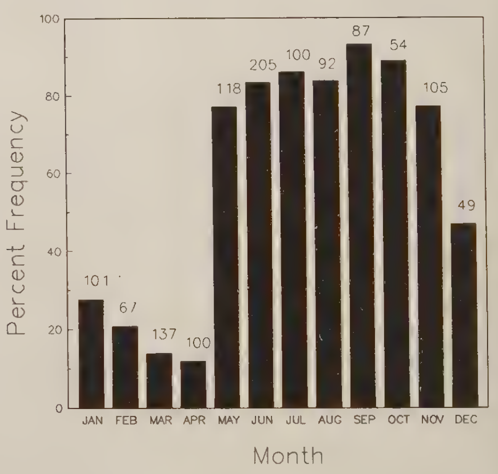

Figure 1
Frequency of light-colored edges (rapid growth period) for broken and burnt otoliths from shortbelly rockfish by month. Sample sizes are shown above each bar.

Parameter estimates were obtained using nonlinear regression analysis (SAS Institute Inc. 1987). Growth equations were fitted separately for males and females and compared using the Extra Sum of Squares Principle (Draper and Smith 1981, Ratkowsky 1983).

To calculate potential yield, we estimated natural mortality (M) using several methods: (1) a regression equation relating maximum observed age and total mortality (Z, which equals M in this case) (Hoenig 1983); (2) an exponential model, in which the estimate of Z was based on both maximum observed age and sample size (Hoenig 1983); and a regression equation relating M to water temperature, average maximum length, and growth completion rate (Pauley 1980). We used mean annual temperature for Ascension Canyon at a depth of 200 meters (8°C, Lynn et al. 1982). We did not estimate M using a catch curve (Ricker 1975) because shortbelly rockfish size tends to increase with depth and latitude (Lenarz 1980). For that reason, our opportunistic samples would not be expected to produce an unbiased estimate of the true age distribution.

Results and discussion

Age and growth

The edge-type analysis of broken and burnt otoliths supported our interpretation that marks were formed annually, generally between December and April (Fig. 1). This was similar to the findings of Kimura et al. (1979) for yellowtail rockfish *S. flavidus* and one month earlier than for widow rockfish *S. entomelas* (Lenarz 1987).

Between- and within-reader agreement was higher for shortbelly rockfish than for other rockfish species. Between-reader agreement was 76% to the year and 87% within one year; within-reader agreement was 77% to the year and 95% within one year (Fig. 2). Using whole otoliths, Six and Horton (1977) reported between-reader agreement for yellowtail rockfish *S. flavidus* to be 24% to the year and 71% within one year. For canary rockfish *S. pinniger*, Six and Horton (1977) reported within-reader agreements of 37 and 21% to the year for whole and sectioned otoliths, respectively. The higher levels of agreement for shortbelly rockfish could be due in part to their relatively young age, as percent agreement declined with increasing age beyond about age 4 (Fig. 2).

The comparison between ages derived from examination of the otolith surface and from broken and burnt halves revealed a systematic bias for fish older than age 4. Ages obtained from the otolith surface tended to be less than ages obtained from broken and burnt otoliths (Fig. 3). Beamish (1979) and Stanley (1986) reported similar results for Pacific ocean perch *S. alutus*.

Shortbelly rockfish live substantially longer than previously reported. The oldest fish we found was 22 years old as opposed to the previous estimate of 12 years (Lenarz 1980). There have been similarly large revisions in estimated maximum age of commercially important groundfish species off the west coast of Canada (Beamish and McFarlane 1987). Only 2 of 23 species were estimated to have maximum ages less than 20 years, and 13 *Sebastes* spp. (not including *S. jordani*) had maximum ages ranging from 36 to 140 years (Beamish and McFarlane 1987).

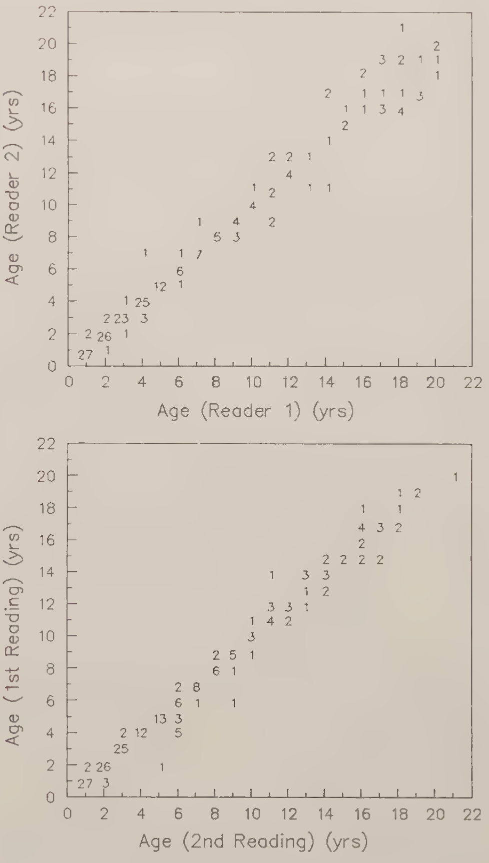

Figure 2
Between-reader (upper panel) and within-reader (lower panel) agreement for shortbelly rockfish ages determined from 200-fish subsamples using broken and burnt otoliths. Numbers at each point refer to number of otoliths examined.

Fitted growth curves differed significantly by sex, with males having a slower growth rate and a smaller maximum size ($F_{crit}(3, 1000, 0.01) = 3.80$, $F_{calc} = 115.23$) (Fig. 4). Although sample sizes were small, there was some evidence that the oldest females were smaller than somewhat younger females (Fig. 4). This could be due to shrinkage in older fish through senescence (Liu and Walford 1969); natural selection favoring small, older fish that use available energy for reproduction rather than continued growth (Leaman and Beamish 1984); or higher mortality for faster-

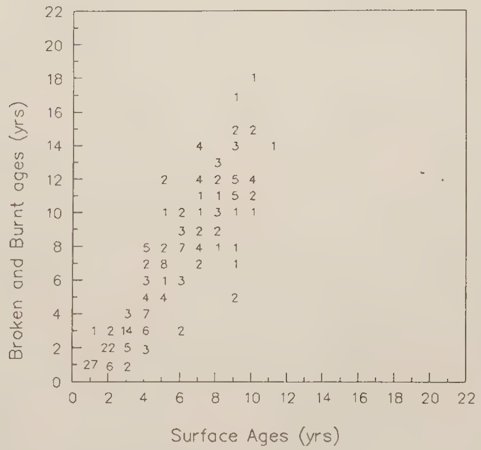

Figure 3
Shortbelly rockfish ages derived from broken and burnt otoliths and from surface readings of whole otoliths from a 200-fish subsample. Numbers at each point refer to the number of otoliths examined.

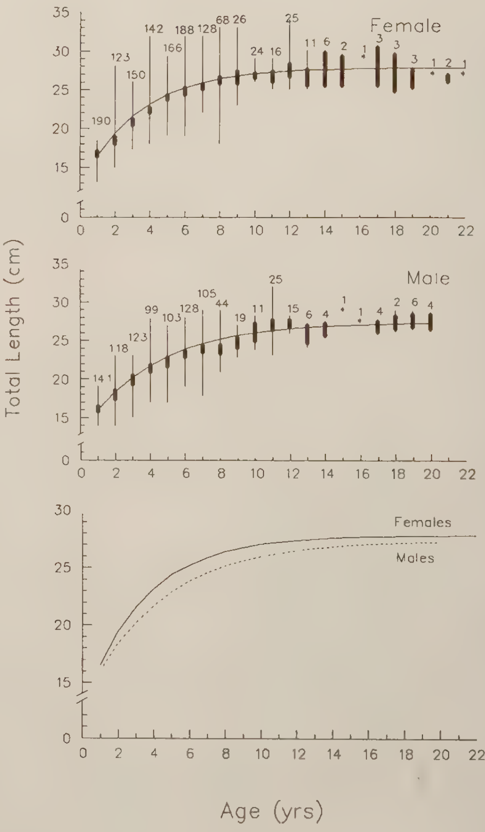

Figure 4
Mean length-at-age and fitted von Bertalanffy growth curves for male and female shortbelly rockfish (upper two panels) (range of values = thin line; 1 SE range = thick line, asterisks = length at which only a single fish was sampled; numbers above each line = sample size). The lower panel facilitates comparison of the sex-specific growth curves.

growing fish (e.g., due to size-selective fishing mortality). The same trend has been observed for yellowtail rockfish and Pacific ocean perch *S. alutus* (Leaman and Beamish 1984).

Our fitted von Bertalanffy growth curves (Table 2, Fig. 4) differed considerably from those reported by Lenarz (1980) and Phillips (1964). Our L_∞ values (Table 2) were lower than the estimates obtained from whole otolith ages (Lenarz 1980) or the combined-sex estimate obtained from scales (Phillips 1964). The decreases in L_∞ as maximum age increased are consistent with Hirschhorn's (1974) observation that a change in the range of ages used to fit the von Bertalanffy growth curve can result in changes to the parameter estimates. Wilson (1985) reported that use of the broken and burnt technique on *S. diploproa* and *S. pinniger* significantly altered von Bertalanffy parameter estimates. Our estimate of k for males was lower than that reported by Lenarz whereas the value for females was higher. The combined-sex estimate of k reported by Phillips (1964) was greater than either estimate obtained in this study. These differences in growth rate may be due to the increase in maximum age as well as differences in depths and areas sampled.

Table 2
Estimates of the von Bertalanffy growth parameters from scales, whole otoliths, and broken and burnt otoliths. Note: Phillips (1964) did not report separate values by sex; Lenarz (1980) did not report t_0 values.

Method	Sex	L_∞(mm)	t_0(yr)	k(yr^{-1})	Source
Scales	Combined	315	−0.270	0.275	Phillips (1964)
Whole otoliths	Male	290	—	0.298	Lenarz (1980)
	Female	324	—	0.211	
Broken and burnt otoliths	Male	279	−3.649	0.184	Present study
	Female	281	−2.514	0.253	

Natural mortality

Using Hoenig's (1983) regression equation, we estimated that M = 0.212 for males and 0.203 for females. We obtained higher estimates using Hoenig's (1983) exponential model (males 0.378, females 0.374) and Pauley's (1980) regression equation (males 0.356, females 0.437). Our sample sizes used in Hoenig's exponential model may have been overestimates (relative to true simple random samples from the population) because of the within-tow correlation. The effective sample size would probably be between 48 (the number of tows) and the number aged per sex (males 959, females 1279). Given the uncertainty of the above estimates, we assume that 0.20–0.35 is a reasonable range for M until a catch-curve estimate can be made. Catch-curve estimates for other *Sebastes* spp. from British Columbia waters were lower, ranging from 0.03 to 0.10 with a range of maximum observed ages from 32 to 77 years (Leaman 1986). Based on a catch-curve analysis, Lenarz and Hightower (1985) estimated that M for widow rockfish *S. entomelas* off Washington–Oregon–California ranged from 0.15 to 0.20. Lenarz (1984) reported that the maximum observed age for Washington-Oregon-California widow rockfish was about 45 years.

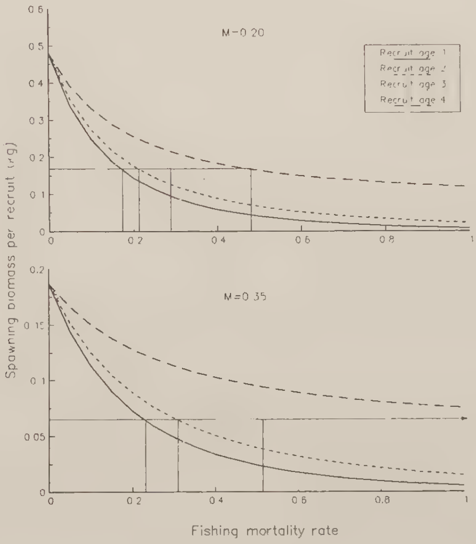

Figure 5

Female spawning biomass per recruit versus fishing mortality rate (F) at two levels of natural mortality (M) and four ages at recruitment. Horizontal lines represent spawning biomass per recruit equal to 35% of the level at F = 0; vertical lines represent the associated F ($F_{35\%}$). $F_{35\%}$ exceeds 1.0 for M = 0.35 and recruitment age of 4 years.

Potential yield

The historical estimate of maximum sustainable yield (MSY), 44,250 t, was based on the relationship MSY = $0.5MB_0$ (Gulland 1971), where B_0 was an estimate of virgin biomass (PFMC 1982). The MSY estimate was based on an assumed M of 0.275 and the 1977 survey estimate of Ascension Canyon to Farallon Islands area biomass (295,000 t) (E. Nunnely, NMFS Alaska Fish. Sci. Cent., Seattle, WA 98115-0070, pers. commun., Jan. 1989).

Our revised estimates of MSY were obtained from a more conservative model ($0.3MB_0$) that Gulland proposed because the former equation was thought to overestimate MSY (Gulland 1983). We used M = 0.20–0.35 and the average of the 1977 and 1980 Ascension Canyon to Farallon Island area biomass estimates (223,850 t). The revised estimates of MSY (13,431–23,504 t) should be viewed as highly preliminary, given that the 1977 and 1980 biomass estimates had confidence intervals in excess of 50% and were not significantly different.

The above estimates of MSY were based on the assumption that the fishing mortality rate (F) that produces MSY would be about equal to M. An alternative approach for obtaining a recommended F would be to determine the fishing mortality rate that reduced spawning biomass per recruit to 35% of the unfished level ($F_{35\%}$). That criterion is being used to manage most of the stocks in the Washington-Oregon-California groundfish fishery (PFMC 1990). Following Ricker's (1975) yield-per-recruit analysis, we calculated spawning biomass per recruit assuming M = 0.20 or 0.35 and linearly increasing maturity. Wyllie Echeverria (1987) reported that 50% of female shortbelly rockfish were sexually mature at age 2 and 100% at age 4. Those estimates were based on whole otolith ages; however, we found relatively good agreement between whole and broken-and-burnt otolith ages through age 4 (Fig. 3). The estimates of $F_{35\%}$ were similar to M if recruitment occurred at about age 2 (Fig. 5). Because shortbelly rockfish mature at a young age, estimates of $F_{35\%}$ increased considerably if recruitment was delayed. These results suggest that assuming F = M when calculating potential yield should provide protection for the spawning stock.

Our estimates of MSY for the Ascension Canyon to Farallon Island area are greater than the current (coastwide) acceptable biological catch (13,000 t) established to permit development of a fishery (PFMC 1989);

therefore, a change in acceptable biological catch does not appear to be necessary to protect the stock. Estimates of shortbelly rockfish abundance (and potential yield) to the north and south of the surveyed area may not be feasible prior to development of a fishery. However, the limited data available suggest that other aggregations may exist. In a study of larval rockfish distributions from Baja California to Bodega Bay, California; MacGregor (1986) found that shortbelly rockfish larvae were most abundant in the Ascension Canyon to Farallon Islands area (49%). He also detected a large concentration in the Channel Islands off southern California (35%), suggesting the presence of a large number of adults in that area. Gunderson and Sample (1980) examined the distribution of pelagic adult rockfish from southern California to Vancouver, British Columbia. They found the highest concentration of shortbelly rockfish in the Ascension Canyon to Farallon Islands area but also detected concentrations in the Channel Islands, in the Point Sur area of California, and off Bodega Bay, California. A smaller concentration was found off the Columbia River in Oregon. These observations suggest that our estimates of MSY are conservative when applied coastwide. More refined estimates of potential yield should be possible once a fishery develops or once planned larval production surveys of the Ascension Canyon to Farallon Islands area have been conducted.

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Citations

Beamish, R.J.
1979 New information on the longevity of Pacific ocean perch *Sebastes alutus*). J. Fish. Res. Board. Can. 36:1395–1400.

Beamish, R.J., and G.A. McFarlane
1987 Current trends in age determination methodology. *In* Summerfelt, R.C., and G.E. Hall (eds.), The age and growth of fish, p. 15–42. Iowa State Univ. Press, Ames.

Boehlert G.W., and M.M. Yoklavich
1984 Variability in age estimates in *Sebastes* as a function of methodology, different readers, and different laboratories. Calif. Fish Game 70(4):210–224.

Chilton, D.E., and R.J. Beamish
1982 Age determination methods for fishes studied by the groundfish program at the Pacific Biological Station. Can. Spec. Publ. Fish. Aquatic Sci. 60, 102 p.

Draper N., and H. Smith
1980 Applied regression analysis, 2d ed. John Wiley, NY, 709 p.

Gulland, J.A.
1971 Science and fishery management. J. Cons. Cons. Int. Explor. Mer 33:471–477.
1983 Fish stock assessment. John Wiley, NY, 223 p.

Gunderson, D.R., and T.M. Sample
1980 Distribution and abundance of rockfish off Washington, Oregon, and California during 1977. Mar. Fish. Rev. 42(3-4): 2–16.

Hirschhorn, G.
1974 The effect of different age ranges on estimated Bertalanffy growth parameters. *In* Bagenal, T.B. (ed.), The ageing of fish, p. 192–199. Iowa State Univ. Press, Ames.

Hoenig J.M.
1983 Empirical use of longevity data to estimate mortality rate. Fish. Bull., U.S. 81:898–903.

Kato, S.
1981 Checking out shortbelly rockfish Colintino Rose II's mission accomplished. Pacific Fishing, Nov. 1981, p. 96–100.

Kimura, D.K., R.R. Mandapat, and S.L. Oxford
1979 Method, validity, and variability in the age determination of yellowtail rockfish, *Sebastes flavidus*, using otoliths. J. Fish. Res. Board Can. 35:377–383.

Leaman, B.M.
1986 Incorporating reproductive value into Pacific Ocean perch management. *In* Proc., Int. Rockfish Symp., Anchorage, Alaska, Oct. 1986, p. 355–368. Lowell Wakefield Fish. Symp. Ser. 5, Alaska Sea Grant, Univ. Alaska, Fairbanks.

Leaman, B.M., and R.J. Beamish
1984 Ecological and management implications of longevity in some northeast pacific groundfishes. Int. North Pac. Fish. Comm. Bull. 42:85–97.

Leaman, B.M., and D.A. Nagtegaal
1987 Age validation and revised natural mortality rate for yellowtail rockfish. Trans. Am. Fish. Soc. 116:171–175.

Lenarz, W.H.
1980 Shortbelly rockfish, *Sebastes jordani*: A large unfished resource in waters off California. Mar. Fish. Rev. 42:(3-4): 34–40.
1984 Status of the widow rockfish fishery. Appendix 4. *In* Status of the Pacific Coast groundfish fishery and recommendations for management in 1985. Pac. Fish. Manage. Counc., Portland.
1987 Ageing and growth of widow rockfish. *In* Lenarz, W.H., and D.R. Gunderson (eds.), Widow rockfish proceedings of a workshop, Tiburon, California, December 11–12, 1980, p. 31–36. NOAA Tech. Rep. NMFS 48.

Lenarz, W.H., and J.E. Hightower
1985 Status of the widow rockfish fishery. Appendix 3. *In* Status of the Pacific Coast groundfish fishery through 1985 and recommended acceptable biological catches for 1986. Pac. Fish. Manage. Counc., Portland, 23 p.
1988 Status of the widow rockfish fishery. Appendix C. *In* Status of the Pacific Coast groundfish fishery through 1988 and recommended acceptable biological catches for 1989. Pac. Fish. Manage. Counc., Portland, 52 p.

Liu, R.K., and R.L. Walford
1969 Laboratory studies on lifespan, growth, ageing, pathology of the annual fish (*Cynolebias bellottii* Steindacher). Zoologica (NY) 54:1–16.

Lynn, R.J., K.A. Bliss, and L.E. Eber
1982 Vertical and horizontal distributions of seasonal mean temperature, salinity, sigma-T, stability, dynamic height, oxygen, and oxygen saturation in the California Current 1950–1978. Calif. Coop. Oceanic Fish. Invest. Atlas 30, 513 p.

MacGregor, J.S.

1986 Relative abundance of four species of *Sebastes* off California and Baja California. Calif. Coop. Oceanic Fish. Invest. Rep. 27:121–135.

Okada, M., T. Machino, and S. Kato

1989 "Bone-softening," a practical way to utilize small fish. Mar. Fish. Rev. 50(3):1–7.

Pauley, D.

1980 On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. Cons. Cons. Int. Explor. Mer. 39(2): 175–192.

PFMC (Pacific Fishery Management Council)

1982 Final fishery management plan and supplemental environmental impact statement for the Washington, Oregon, and California groundfish fishery. Pac. Fish. Manage. Counc., 248 p.

1989 Status of the Pacific coast groundfish fishery through 1989 and recommended acceptable biological catches for 1990. Pac. Fish. Manage. Counc., 299 p.

1990 Status of the Pacific coast groundfish fishery through 1990 and recommended acceptable biological catches for 1991. Pac. Fish. Manage. Counc., 661 p.

Phillips, J.B.

1964 Life history studies on ten species of rockfish (genus *Sebastodes*). Calif Dep. Fish Game, Fish Bull. 126, 70 p.

Ratkowsky, D.A.

1983 Nonlinear regression modeling. Marcel Dekker, NY, 276 p.

Ricker, W.E.

1975 Handbook of computations for biological statistics of fish populations. Fish. Res. Board Can., Bull. 1:235–264.

SAS Institute Inc.

1987 SAS/STAT guide for personal computers, Version 6 Edition. SAS Inst. Inc., Cary, NC.

Six, L.D., and H.F. Horton

1977 Analysis of age determination methods for yellowtail rockfish, canary rockfish, and black rockfish off Oregon. Fish. Bull., U.S. 75:405–414.

Stanley, R.D.

1986 A comparison of age estimates derived from the surface and cross-section methods of otolith reading for Pacific ocean perch (*Sebastes alutus*). *In* Proc., Int. Rockfish Symp., Anchorage, Alaska, Oct. 1986, p. 187–196. Lowell Wakefield Fish. Symp. Ser. 5, Alaska Sea Grant, Univ. Alaska, Fairbanks.

Wilson, C.D.

1985 The effects of different otolith ageing techniques on estimates of growth and mortality for two species of rockfishes, *Sebastes pinniger* and *Sebastes diploproa*. M.S. thesis, Oregon State Univ., Corvallis, 169 p.

Wyllie Echeverria, T.

1987 Thirty-four species of California rockfishes: Maturity and seasonality of reproduction. Fish. Bull., U.S. 85:229–250.

Wyllie Echeverria, T., W.H. Lenarz, and C. Reilly

1990 Survey of the abundance and distribution of pelagic young-of-the-year rockfishes off central California. NOAA Tech. Memo. NOAA-TM-NMFS-SWFC-147, NMFS Southwest Fish. Sci. Cent., La Jolla, CA, 125 p.

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WHAT CAN BE DONE ABOUT CONFLICTS BETWEEN MARINE MAMMALS AND FISHERIES?

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ABSTRACT

Conflicts between marine mammals and fisheries are of two sorts: those in which the mammals harm the fishery, and those in which the fishery harms the mammals. Examples of each are presented. Potential reasons to conserve marine mammals include their value as fishery resources, as parts of complex natural systems, as resources for tourism and education and as unique biological entities deserving continued existence. Marine mammal populations are highly vulnerable to depletion because of low reproductive rates. Possible solutions to conflicts include closing the fishery, removing the mammals, scaring or warning the mammals away, releasing entangled mammals, closing areas to fishing, closing seasons to fishing, modifying fishing gear, modifying fishing practices, and setting safe limits on mammal kills. Examples of each are given. A series of steps that can be followed in resolving conflicts are presented.

INTRODUCTION

The purpose of this paper is to review the question of conflicts between marine mammals and fisheries in general and to offer examples of how such conflicts might be resolved. I will address three questions:

1) What are the conflicts?

2) Why worry about the marine mammals?

3) What can be done?

WHAT ARE THE CONFLICTS?

Marine mammals cause problems for fisheries, and fisheries cause problems for marine mammals. A few examples of each kind of conflict follow; there are many more.

Marine mammals causing problems for fisheries

Killer whales in Alaska

Killer whales (*Orcinus orca*) eat many of the same fish that humans eat, and sometimes they decide that it's easier to let humans catch the fish for them than it is to catch the fish themselves. This, of course, makes the fishermen unhappy. This has happened in Alaska, in the bottom longline fishery for blackcod, *Anoplopoma fimbria*, in the Gulf of Alaska and Bering Sea (Dahlheim, 1988; Holleman, 1988).

The U.S. blackcod fishery began in the early 1980s and is still expanding. The fishermen set the longlines on the bottom at depths of 400-1100 meters. The longlines are typically 3.5-7 kilometers meters long, with hooks at about 1-meter intervals.

The fishermen first reported damage to catch by killer whales in 1985, in Prince William Sound. Only one pod of killer whales was involved at first. The behavior has since spread to other pods and other areas. The whales bite off the bodies of the blackcod while the longline is being retrieved, leaving only the head. They gather at the buoy markers when a fishing vessel approaches, waiting for the fishermen to haul the longline.

The damage has been considerable. About 20% of the catch is taken by killer whales in some areas. The cost to the fishermen averages about $2,300 per day. The total loss since the problem began may be over a million dollars.

The fishermen tried to solve the problem themselves. They tried many methods to scare or trick the whales, including seal bombs, decoy boats, night fishing, shooting, explosives, electricity and other things. Some of this was illegal, of course. The State of Alaska tried other things, but without much success. In the last two or three years, the problem has diminished in some areas, possibly because the individual whales doing most of the thieving have been killed by the fishermen. Meanwhile, research continues.

Sea otter in California

The sea otter, *Enhydra lutris*, is a very attractive and endearing animal. Unfortunately, it too likes to eat what humans eat, in this case abalone.

The sea otter was almost exterminated in California by fur hunters in the 19th Century (Kenyon, 1981). Since the late 1930s, a small remnant population has grown and re-expanded the range to much of the coast of central California. As this happened, the otters moved into areas that had been free of otters for many years. The abalone populations in these areas were very high because of the otters' absence. The high abalone populations had supported very valuable fisheries. When the otters came, the abalone became very scarce. Not only did the abundance decrease, but the average size also decreased greatly. Where sea otters are present in large numbers, only the small abalone that can get into crevices beyond the reach of sea otters survive.

Abalone populations in California overall have fluctuated for a variety of reasons, including overfishing, but there can be no doubt that sea otters and commercial abalone fisheries are incompatible (Estes and VanBlaricom, 1985). In California, environmentalists have formed an organization called Save Our Shellfish (S.O.S.), and the fishermen have formed a group called Friends of the Abalone.

Dolphins in Japan

Dolphins and small whales affect fisheries in Japan in a number of ways (Kasuya, 1985). They damage fishing gear, take fish from hooks and nets and are reported to disperse fish schools or cause the fish to stop feeding. The main cetaceans involved are the bottlenose dolphin (*Tursiops truncatus*), the false killer whale (*Pseudorca crassidens*), Risso's dolphin (*Grampus griseus*) and the Pacific white-sided dolphin (*Lagenorhynchus obliquidens*). The greatest effect is on the yellowtail (*Seriola dorsalis*) and squid fisheries at Iki Island and other neighboring islands. This has been known since the early part of the century, and the fishermen and the local government have been trying to deal with the problem since that time.

In the mid-1970s, after other remedies had been tried, large culls began at Iki Island, and the situation came to the attention of the world. The picture has been confused by two scientific findings: some of the fish stocks in the region may be declining due to overfishing, and examination of stomach contents of the dolphins and whales has shown that only one of them, the false killer whale, feeds on yellowtail.

Seals and sea lions in California

Seals and sea lions interfere with fisheries around the world. In California, the main species are the harbor seal (*Phoca vitulina*), which you see here, and the California sea lion (*Zalophus californianus*). Nearly all of the direct damage to catch and gear in California is caused by these two species.

The most severe damage is to the catch. This table (from DeMaster et al., 1985) shows the estimated annual value of fish and gear stolen or damaged by marine mammals in California in 1979-81. The estimated annual total is about $600,000. The largest financial loss reported was in the commercial salmon trolling fishery. A minimum loss of $130,000 was estimated for the month of May, 1980; this did not include damage to gear.

Fisheries causing problems for marine mammals

Tuna fishery in the eastern Pacific

The tuna purse-seine fishery in the eastern tropical Pacific has killed millions of dolphins in the last 30 years (Allen, 1985).

The fishermen seek out the dolphin schools and set their nets on them in order to catch the tuna that associate with the schools. The main dolphins involved are the spinner dolphin (*Stenella longirostris*) and the pantropical spotted dolphin (*Stenella attenuata*). Many of the dolphins become entangled in the folds of the net and suffocate. The dead dolphins are discarded.

The dolphin kill declined in the 1970s from its very high level of nearly a half million annually in the early 1960s. In the mid 1980s, it went up again. Earlier on, most of the kill was by the United States fleet, but in recent years most of the kill has been by the vessels of other nations, including Mexico, Venezuela, Ecuador and others (data from Inter-American Tropical Tuna Commission, Nov., 1990).

Gillnet fisheries in the western North Atlantic

Harbor porpoise seem especially vulnerable to being entangled in gillnets. One example of this is along the east coasts of the U.S. and Canada, where there are several gillnet fisheries for cod, hake and pollack. The nets are set on the bottom and vary between 450 to 2000 meters in length. There are thousands of vessels, each setting about 5 km of net a day (Read, 1990).

It is estimated that the fisheries kill 300-800 harbor porpoise a year. This is 4-10% of the estimated population of 8000 porpoises. With this pressure, the population will almost certainly decline.

Driftnet fisheries in the North Pacific

Several hundred driftnet boats operate in the North Pacific. They come from Japan, Taiwan and Korea and fish mainly for squid, tuna, pomfret and salmon. Each boat fishes as much as 50 km of net a day, making the total in a year several million km of net. These nets kill dolphins, porpoises, whales, birds, turtles, sharks and unwanted fish (Jones et al., 1990).

One of the dolphins killed in large numbers is the northern right whale dolphin (*Lissodelphis borealis*). A very crude estimate of total kill of the right whale dolphin is 18,000 a year (IWC, in press). (It must be stressed that this estimate is based on extrapolation from a very small sample of data that may not be representative of the entire fisheries.) The population size is unknown, therefore the impact of the incidental kill on the population is also unknown.

Coastal fisheries in Peru

Coastal fisheries of a wide variety in Peru have grown tremendously since the collapse of the anchoveta fishery, which was the largest fishery in the world, a few years ago put many fishermen out of work. These fisheries use small gillnets and purse seines. As bycatch, they kill dusky dolphins (*Lagenorhynchus obscurus*), Burmeister's porpoise (*Phocoena* *spinipinnis*) and common dolphins (*Delphinus delphis*) in large numbers and smaller numbers of many other species (Reyes and Oporto, 1990).

The dolphins and porpoise that the fishermen catch go to the market. The public has developed a taste for them, so now the fishermen go out to hunt dolphins, using nets and harpoons. Something more than 1800 dusky dolphins are killed by boats operating out of the major fishing ports. Since the structure and size of the dolphin populations are unknown, the impact is unknown.

WHY WORRY ABOUT THE MARINE MAMMALS?

A logical question is, why worry about marine mammals? We know why we should worry about the fisheries; many of us depend on them for a living, and our nations depend on them for food. But why should we worry about the marine mammals? People's attitudes toward marine mammals vary a great deal. Some people view marine mammals as requiring complete protection. Others view them only as something to eat or as nuisances to be eliminated. In any case, most of us would agree that there are several potential reasons to care about what happens to marine mammals, even if we don't agree on their relative importance.

1) Marine mammals themselves are fishery resources.
Marine mammals are not eaten just by Eskimos. They are also eaten in Japan, India, Sri Lanka, Peru, Norway, Spain, France, Greenland, Canada, the Soviet Union, the United States and many other countries, not by everyone, but by some people (Report of the IWC, 1980-1990; IWC, in press). If we drive a population of marine mammals to extinction, then we eliminate forever the possibility of using it as such a resource.

2) Marine mammals function as parts of natural systems.
Marine mammals are parts of complex ecological systems. We cannot always predict what will happen when we remove part of such a system. For example, what would happen to the valuable tuna fisheries in the eastern tropical Pacific if the dolphins the tuna associate with were removed? Would the tuna be able to find enough food on their own? Would the fishermen be able to find the tuna?

In another example, gray whales may be very important to the bottom ecology of the Bering Sea because of their feeding behavior (Nerini, 1984; Oliver, 1983). The conditions they create by constantly digging up the bottom may promote productivity. What would happen to the valuable fisheries in the Bering Sea if the ecosystem there were disturbed by removal of the gray whales?

There are many more such examples; in some cases cetaceans may even benefit fishermen by eating species that could compete with fishermen for commercially valuable fish (Katona and Whitehead, 1988).

3) Marine mammals have value for tourism and education.
Another reason to worry about marine mammals is that they can be very valuable for tourism and education. The whale-watching industry is worth millions of dollars annually in California (Tilt, 1986) and is growing rapidly in other places, including Japan and Norway.

4) Marine mammals, like other creatures, deserve to exist and should not be killed unnecessarily.
Many people worry about marine mammals because they believe that they should not be killed. This must be included in the list of potential reasons for the government to worry about the welfare of marine mammals.

Marine mammal populations are very easily depleted.
If we accept any of these reasons to worry about marine mammals, then we must consider two important facts about them. First, marine mammal populations are very easily depleted (IWC, in press). This is mainly because of their low reproductive rates. They are not like fish, which can produce thousands of eggs at a time. They are more like humans; they produce one calf a year at a maximum. Pregnancy lasts 10 to 15 months, depending on the species. The usual interval between births in dolphins is two years or more. The calf may nurse for more than a year. Dolphins are not sexually mature until they are about 6-12 years old, depending on the species. The result of all this is that most dolphin populations cannot stand kills of more than a few percent a year, or even less; more than that and the population declines.

Depleted marine mammal populations require a very long time to recover.
The second caution is that this low reproductive rate means that recovery of a depleted population is very slow. The damage that is done by a fishery in a year or two could take generations to repair.

In some cases, it may not be possibly to restore a depleted population. For example, the blue whale has completely protected in the Antarctic since the 1960s, but it has not recovered; numbers are still very low (Perrin, 1989). It may never recover; the food resources that it used in the past may now be important to other animals that increased in number after depletion of the blue whale. These possible replacements include crabeater seals, penguins and perhaps other, smaller whales. The system may arrive at a new balance that does not include a lot of blue whales. This tells us that in some cases it may not ever be possible for a depleted population to recover; once it's gone, it may be gone forever.

WHAT CAN BE DONE ABOUT THE CONFLICTS?

If we believe that both fisheries and marine mammals are worth worrying about, then we must consider how to resolve the existing conflicts between them. There have been many attempts at solutions in a number of places. Some have worked; others have not. A partial list:

1) *Close the fishery.*
2) *Remove the mammals (cull or translocate).*
3) *Scare the mammals away.*
4) *Release the mammals.*
5) *Close areas to fishing.*
6) *Close seasons to fishing.*
7) *Modify fishing gear.*
8) *Modify fishing practices.*
9) *Set safe limits on mammal kills.*

Examples of each of these follow:

1) Close the fishery.

One example of a fishery closure is what happened to the driftnet swordfish fishery in Italy. The fishery killed thousands of cetaceans, including the sperm whale you saw a minute ago. Hundreds of them washed up on the beaches. The Italian Government last year banned the fishery, because of public pressure (IWC, in press).

Another example is the coastal gillnet fishery for halibut in California. This fishery kills harbor porpoise and other marine mammals (Heyning et al., 1990;Barlow et al., in press; Fulton, 1989). The people of California voted last year to close the fishery and buy out the boats.

In these examples, the mammals are now protected, but the fisheries, of course, are gone or will be gone, jobs will be gone, and fish prices may go up for the consumer.

2) Remove the mammals.

One example of the removal of marine mammals in conflict with fisheries, of course, is the cull at Iki Island in Japan. This was an extreme measure, and the consensus now is that it probably was not effective.

Alternatives to killing the mammals are to prevent them from entering the fishery area or translocate them. This approach is being used in southern California for the sea otter. The otter population is presently being prevented from expanding to the south, in order to maintain an otter-free zone in which abalone, clam, oyster and sea-urchin fisheries can continue. When otters stray into the fishery zone, they are captured and moved back to the otter zone. This scheme has not been in use long enough yet for us to know if it is going to work. It is a compromise between those who don't care much about the otters and those who don't care much about the fisheries. The recovery plan for otters in California also includes the establishment of a new population at San Nicolas Island (Fulton, 1988).

3) Scare the mammals away.

Most attempts to warn or scare the marine mammals away from the fishing operation, to prevent either theft of the catch or entanglement of the mammals, have been failures. This did work in one case in Alaska, where killer whale sounds have been used to prevent white whales (*Delphinapterus leucas*) from entering a salmon stream (Fish and Vania, 1971).

In another example, there are plans to use acoustic alarms to warn humpback whales away from cod traps in Newfoundland (Lien et al., 1990). The whales apparently recognize the alarms, and the hope is to condition them to associate the alarms with the dangerous nets. This is possible because the whales are very large and strong and most of the time escape alive from entanglements.

There are many cases where the alarm approach has been tried but failed. These include the tuna fishery in the eastern tropical Pacific, where we tried killer whale sounds, and at Iki Island, where a variety of noises and sound devices were tried. Another place the approach has failed is in the salmon driftnet fishery in the North Pacific (Hatekeyama et al., 1990). The usual problem is that the mammals react to the sounds initially but soon accomodate to them and ignore them. The animals are relatively intelligent and quickly understand that the noises are harmless. The noises may actually act as beacons to attract the marine mammals to the netted fish. And the dolphins and porpoises that become entangled do not learn to associate the warning with the dangerous nets, because they are unable to escape and they die (IWC, in press).

4) Release the mammals.

One way to reduce the number of marine mammals dying in nets is to rescue as many as possible from the nets. This is required in the U.S. tuna fishery in the eastern Pacific, where about 99% of all the dolphins captured are now released alive (data from Porpoise Rescue Foundation, 1987) compared to about 80% in the 1960s (Perrin, 1970). This has also helped in California, where several gray whales have been cut loose from gillnets and in Newfoundland, where nearly all humpback whales entangled in cod traps are now released alive pers. comm. from John Lien, 1990).

Of course, for best success this approach requires that the net be closely tended, because mammals entangled below the surface will quickly drown if not released.

Rescuing large whales is difficult and dangerous. A special program has been set up in Newfoundland to train and equip the fishermen to do this, and the IWC has recommended that similar programs be established elsewhere (IWC, in press).

5) Close areas to fishing.

If large kills of marine mammals occur in only part of the area of operation of a fishery, then the kill can be eliminated or reduced by keeping the fishery out of that area. This was successful in reducing the incidental kill of sea otters in Central California. The gillnetters were prohibited from setting their nets in very shallow water near shore. The kill of sea otters dropped a great deal very rapidly (Fulton, 1985).

This approach has also been effective around the Channel Islands in California, where fishermen have been prohibited from setting their nets in shallow water near seal and seal lion rookeries. This has reduced the incidental kill of pinnipeds. The fishery still exists but operates elsewhere.

6) Close seasons to fishing.

If the marine mammals migrate through an area or live there only part of the year, then a seasonal closure of the area to a fishery can reduce the incidental kills. This has been successful in New Zealand, where gillnetting has been banned in waters around Banks Peninsula during the part of the year when Hector's dolphins (*Cephalorhynchus hectori*) are most common there (Dawson, in press).

In California, waters along the migration route of the gray whale (within 25 miles of shore) are closed to driftnetting during the migration season. This has resulted in a lower frequency of entanglements (LaGrange, 1990).

7) Modify fishing gear

There have been many attempts to reduce kills of marine mammals by modifying the fishing gear. Some of these have succeeded and others have failed.

One success has been in the tropical tuna fishery in the eastern Pacific. The entanglement rate has been lowered by using smaller mesh webbing in parts of the seines and by modifying part of the net to allow the dolphins to escape more easily during rescue operations. These changes, together with a requirement that live animals in the net be rescued, has reduced the U.S. dolphin kill rates by a factor of 10 over the last 20 years (data from Inter-American Tropical Tuna Commission).

There have been many attempts to make gillnets more detectable for dolphins by making them more "visible" acoustically. Most of these experiments have not been successful. This has been tried in the salmon driftnet fishery in the North Pacific, in the Taiwanese shark gillnet fishery off Australia, and in other fisheries. The problem may be that the dolphins can easily detect the nets but are just too busy pursuing prey and don't pay any attention to them (IWC, in press).

A gear modification that has been successful in California is the use of lighter twine in gillnets. This allows large whales to break free before they drown (LaGrange, 1990).

There is much room for more research to develop fishing gear that is less dangerous to marine mammals.

8) Modify fishing practices

The way in which nets are set can reduce marine mammal kills. For example, in the U.S. tuna fishery in the eastern tropical Pacific, the captains identify the portion of a dolphin school "carrying" the most tuna and try to isolate it from the rest of the school before setting the seine. Thus the number of dolphins captured is lower, but the tuna catch remains high.

There have been several experiments with setting drift nets below the surface rather than at the surface. This was done in the Taiwanese shark fishery off Australia (Hembree and Harwood, 1987). Fewer dolphins were caught, but fewer fish were caught also. The results of similar trials of subsurface nets in the Japanese driftnet fishery for tuna in the South Pacific and squid in the North Pacific have been unconclusive. In this case, the fish catches were unaffected, but it was not clear that the dolphin catch rates were lower (Hayase and Watanabe, 1990). We need more research here.

9) Set safe limits on mammal kills.

Limits or quotas can be set on kills or kill rates. However, in order to know what a safe level is, you must know something about the size and reproductive rates of the mammal population. We usually don't have this information, and it's very expensive to obtain it. It's very difficult to set safe limits; this is one of the reasons that the International Whaling Commission has temperarily halted commercial whaling; we don't know what is safe.

One case where quotas have been used for U.S. fishermen is in the tropical tuna purse-seine fishery. The limits here are not based on population analysis and do not apply to the entire international fleet. The quotas for the U.S. fleet are almost certainly far below levels that would endanger the populations. (However, the takes by the non-U.S. fleets exceed the U.S. take by a wide margin.) U.S. law says that the kills should be as low as practically possible, that no dolphins should be killed unnecessarily. The overall quota of 20,000 dolphins of all species and the quotas for individual species and stocks are based on the kill rates for the more capable captains. In some years, the quotas have been filled before the end of the year, and the U.S. fishermen were prohibited from setting their nets on dolphins for the rest of the year. This approach is valuable because it motivates the fishermen to fish in such a way that they minimize the dolphin kills. The fewer dolphins they kill, the longer they can fish.

We also have quotas for some pinnipeds for U.S. coastal fisheries in the North Pacific. 675 Steller sea lions, (*Eumatopias jubatus*) and 50 North Pacific fur seals (*Callorhinus ursinus*) may be killed annually. We have fairly good estimates of population size for these animals, because they come out on land to bear young.

We hope to be able to set safe mammal kill limits for many other fisheries in the future. We are just now doing the necessary research to estimate what is safe (Barlow et al., in press). There are very many fisheries, so it is a large undertaking. We have classified all of our fisheries into three categories based on mammal kills:

Category I. Those taking marine mammals frequently (more than one in 20 days),

Category II. Those taking them occasionally (one in 20 days), and

Category III. Those with a remote or no liklihood of taking marine mammals (none in 20 days).

Category-1 and Category-2 vessels must obtain permits to continue fishing. Category-I vessels must carry government observers if asked. The Category-1 fisheries have the highest priority in our research to determine what the kill levels are and what is safe.

Choosing an approach

The choice of approach depends on the situation. Each fishery is different, and each problem is different. The choice also depends on the prevailing laws and on the value systems and goals of the people who make and influence the decisions. There can be concern about the mammals and goals at three levels:

1) *Prevent extinction of the species or population.* (Nearly all would agree with this goal, including most fishermen.)

2) *Prevent significant decrease in the population.* (Most of the public and wildlife managers would probably agree with this goal, but most of the fishermen may disagree).

3) *Prevent the killing or harm of any marine mammal, for any reason.*
(This view is held by some of the public but not by others, and usually by very vew fishermen.)

In deciding on a solution, the views, goals and needs of all should be considered. However, damage to some interest may be unavoidable. It may be necessary to close or severely restrict a fishery to save a marine mammal population from extinction or severe depletion. Or, it may be necessary to allow the continued kill of some marine mammals in order to save a valuable fishery. We have had both of these experiences in the United States.

How to proceed

Experience has taught us that there are several logical and necessary steps to take in solving a conflict between marine mammals and fisheries:

1) Determine the nature, extent and monetary costs of the conflict, based on independent and objective observations, data and analyses.

2) Determine the extent, size and status of the marine mammal population(s).

3) Give all involved and interested parties an opportunity to state their needs and views and have their questions answered.

4) Decide what the goals are and what legal requirements must be satisfied.

5) Develop a plan to solve the problem, with time limits and criteria of success for each step.

6) Provide the resources (money, authority, people and equipment) needed to carry out the plan and enforce its provisions.

6) To the extent possible, involve the fishermen, local residents and other interested parties in carrying out the plan.

7) Monitor the results and decide if the plan succeeded.

8) Develop a plan to mitigate any damage done to the fishery, and provide the resources to carry it out.

We have not always carried out all of these steps, or even most, in the United States, of course, and we have had our share of irrational or unwise decisions, delays, failures, and unwanted damage to fisheries and to marine mammal populations. We hope that we will do better in the future; we must try. Our goal is to have both healthy fisheries *and* healthy marine mammal populations.

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REFERENCES

Allen, R. L. 1985. Dolphins and the purse-seine fishery for yellowfin tuna. Pp. 236-252 *in* J. R. Beddington, R. J. H. Beverton and D. M. Lavigne. Marine Mammals and Fisheries. Allen and Unwin, London, 354 p.

Barlow, J., R. W. Baird, J. E. Heyning, K. Wynne, A. M. Manville, II, L. F. Lowry, D. Hanan, J. Sease and V. N. Burkanov. In press. A review of cetacean mortality in coastal fisheries along the west coast of the U.S. and Canada and the east coast of the U.S.S.R. Rep. Int. Whal. Commn. (spec. iss.).

Dahlheim, M. E. 1988. Killer whale (*Orcinus orca*) depredation on longline catches of sablefish (*Anoplopoma fimbria*) in Alaskan waters. NWAFC Proc. Rep. 88-14, 31 p.

Dawson, S. M. In press. Incidental catch of Hector's dolphin in inshore gillnets. Mar. Mamm. Sci.

DeMaster, D., D. Miller, J. R. Henderson and J. M. Coe. 1985. Conflicts between marine mammals and fisheries off the coast of California. Pp. 111-118 *in* J. R. Beddington, R. J. H. Beverton and D. M. Lavigne. Marine Mammals and Fisheries. Allen and Unwin, London, 354 p.

Estes, J. A. and G. R. VanBlaricom. 1985. Sea-otters and shellfisheries. Pp. 187-235 *in* J. R. Beddington, R. J. H. Beverton and D. M. Lavigne. Marine Mammals and Fisheries. Allen and Unwin, London, 354 p.

Fish, J. F. and J. S. Vania. 1971. Killer whale, *Orcinus orca*, sounds repel white whales, *Delphinapterus leucas*. Fish. Bull. 69:531-535.

Fulton, C. 1985. California moves to stop the sea otter drownings - Emergency fishing ban followed by permanent protective legislation. The Otter Raft 33:2.

Fulton, C. 1988. San Nicolas at last! The Otter Raft 38:2-3.

Fulton, C. 1989. Monterey Bay gillnets take tragic toll of sea otters and harbor porpoise. The Otter Raft 41:13.

Hatakeyama, Y., K. Ishii, T. Akamatsu, H. Soeda, T. Shimamura and T. Kojima. 1990. Studies on the reduction of entanglement of Dall's porpoise, *Phocoenoides dalli*, in the Japanese salmon gillnet. IWC meeting doc. SC/O90/G9, 32 p.

Hayase, S., Y. Watanabe and T. Hatanaka. 1990. Preliminary report on the Jpanese fishing experiment using subsurface gillnets in the South and North Pacific, 1989-1990. Abstracts IWC Symp. Mort. Cetaceans in Passive Fish. Nets and Traps, La Jolla, Calif., Oct. 20-21, 1990:14.

Hembree, D. and M. B. Harwood. 1987. Pelagic gillnet modification trials in northern Australian seas. Rep. Int. Whal. Commn. 37:369-373.

Heyning, J. E., T. D. Lewis and C. D. Woodhouse. 1990. Mortalities of odontocetes from gear off southern California. Abstracts IWC Symp. Mort. Cetaceans in Passive Fish. Nets and Traps, La Jolla, Calif., Oct. 20-21, 1990:19.

Holleman, M. S. 1988. Killer whales stalk black cod fishery. Alaska Magazine, Sep. 1988:21-27,52.

IWC. In press. Report of the Workshop on Mortality of Cetaceans in Passive Fishing Nets and Traps, La Jolla, California, 22-25 Oct., 1990. Rep. Int. Whal. Commn. (spec. iss.).

Jones, L., M. Dahlberg and S. Fitzgerald. 1990. High seas driftnet fisheries of the North Pacific Ocean. IWC meeting doc. SC/O90/G43, 17 p.

Kasuya, T. 1985. Fishery-dolphin conflict in the Iki Island area of Japan. Pp. 253-275 *in* J. R. Beddington, R. J. H. Beverton and D. M. Lavigne. Marine Mammals and Fisheries. Allen and Unwin, London, 354 p.

Katona, S. and H. Whitehead. 1988. Are Cetacea ecologically important? Oceanogr. Mar. Biol. Annu. Rev. 26:553-568.

Kenyon, K. W. 1981. Sea otter *Enhydra lutris* (Linnaeus, 1758). Pp. 209-223 *in* S. H. Ridgway and R. J. Harrison (eds.) Handbook of Marine Mammals, Vol. 1 The Walrus, Sea Lions, Fur Seals and Sea Otter. Academic Press, London, 235.

LaGrange, J. 1990. IWC conference on mortality of cetaceans in passive fishing nets and traps, October 1990, La Jolla, California. IWC meeting doc. SC/O90/G45, 5 p.

Lien, J., A. Verhulst, T. Huntsman, J. Jones and R. Seton. 1990. Reactions of humpback whales to novel sounds: curiosity and conditioning. IWC meeting doc. SC/O90/G51, 13 p.

Nerini, M. 1984. A review of gray whale feeding ecology. Pp. 423-450 *in* M. L. Jones, S. L. Swartz and S. Leatherwood (eds.). The Gray Whale *Eschrichtius robustus*. Academic Press, Orlando, 600 p.

Oliver, J. S. 1983. Population and community consequences of gray whale feeding in soft bottoms. Abstracts 5th Bienn. Conf. Biol. Mar. Mamm., Nov. 27-Dec. 1, 1983, Boston, Mass.:75.

Perrin, W. F. 1970. The problem of porpoise mortality in the U.S. tropical tuna fishery. Proc. 6th Ann. Conf. Biol. Son. Div. Mamm.:46-48.

Perrin, W. F. (ed.). 1989. Newsletter of the Cetacean Specialist Group (IUCN) 5, 15 p.

Read, A. J. 1990. Gill net and trap fisheries in the Northwest Atlantic. IWC meeting doc. SC/O90/G6, 34 p.

Reyes, J. C. and J. A. Oporto. 1990. Gillnets, trap fisheries and cetaceans in the South East Pacific. IWC meeting doc. SC/O90/G11, 28 p.

Tilt, W. 1986. Whalewatching comes of age. Whalewatcher 19(2):19.

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Why are there so many kinds of whales and dolphins?

Although the cetaceans are a small group, compared with, say, beetles (thought to have millions of species) or even with some other mammalian orders, such as the rodents (with 1700 species), they include 75–80 species and are extremely diverse morphologically. They range from the generalized dolphins, such as the bottlenose dolphin, *Tursiops truncatus*, to highly derived forms such as the right whale dolphin, *Lissodelphis borealis*, which has no dorsal fin; from river dolphins weighing 20 or 30 kg to leviathans such as the sperm whale, *Physeter macrocephalus*, weighing more than 100,000 kg.

Even 75 species seems to be a lot for such mobile animals. After all, the oceans are continuous. Some dolphins have been recorded as traveling as much as 50–100 km per day. And we know that many whales and dolphins, like other large marine animals such as tunas and sharks, are almost worldwide in distribution. Some of these species are closely related to each other. How did they arise?

One model of speciation in isolation has to do with past climate fluctuations during which cold water may have pinched off the tropical Atlantic one or more times. At present, warm-temperate water flows around the Cape of Good Hope from east to west during the austral summer. This flow provides communication between the tropical Indo-Pacific and the tropical Atlantic. During the austral winter, water around the cape is too cold for tropical cetaceans, as it probably was during the Pleistocene or earlier cold periods. The Cape of Good Hope was probably embedded in very cold water year round. This cold water isolated the tropical Atlantic from the Indo-Pacific and may account for the relatively high degree of endemism in dolphins in the tropical Atlantic. For example, there are two species of spotted dolphin (*Stenella*) in the tropical Atlantic, but only one occurs in other tropical oceans.

In another example, there is one dolphin in the monotypic genus *Sousa* in the subfamily Steninae that ranges from China into the Indian Ocean and up the western coast of Africa. A second, closely related dolphin in another monotypic genus, *Sotalia,* inhabits the coast of northeastern South America and the Amazon and Orinoco rivers. A third dolphin species, still another monotypic genus, *Steno*, lives on the high seas.

The pair of strictly coastal and riverine species is adapted to warm, shallow, murky waters. There is a wide gap in such habitats across the tropical Atlantic, and an even wider expanse of oceanic waters between the Indo-Pacific and the western coasts of the New World.

There are at least two hypotheses for the origin of the two coastal species. In the first, *Sousa* stragglers made it across the Atlantic at least once, long enough ago to result in species-level divergence. In the second hypothesis, the two coastal species arose independently by coastal colonization from the oceanic species. There are other possible permutations of events, but these seem to be the most likely ones.

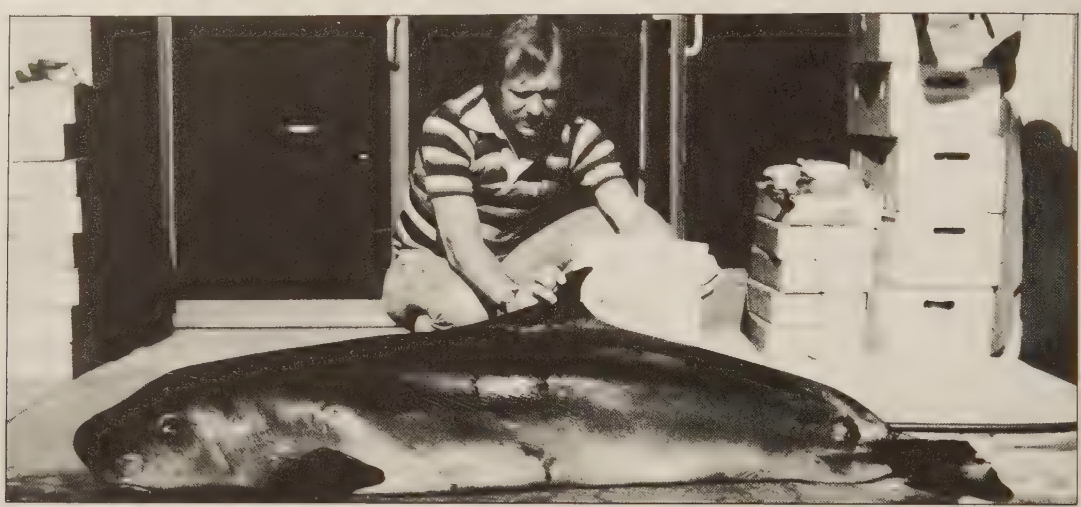
There are other models of isolation and speciation in the Cetacea, including, for example, antitropical isolation (cold water distributions in the Northern and Southern hemispheres separated by warm tropical waters) during warm geological periods. Although marine habitats for mammals are indeed generally more continuous than terrestrial habitats, there has been enough structure and partitioning in the oceans to allow easily for the evolution of the species diversity through allopatric speciation (speciation through isolation).

Another level of diversity in the cetaceans is that below the species level. Wherever we have enough data, we have found pronounced geographical variation within a species. There are some patterns in this: variation between populations in open and enclosed seas, in coastal versus offshore habitats, and in different pelagic habitats in the open sea.

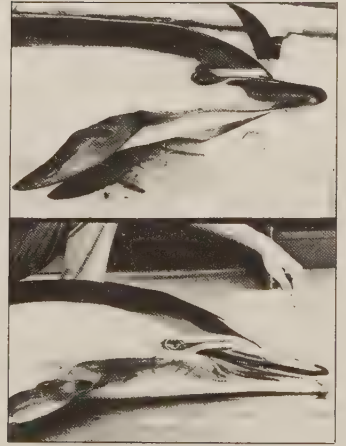
Dolphins tend to be larger in open waters than in closed seas. For example, in the common dolphin (*Delphinus*) in the contiguous waters of the North Atlantic, in the Mediterranean, and in the Black Sea, maximal size is greatest in the North Atlantic, least in the Black Sea, and intermediate in the Mediterranean. The bottlenose dolphin (*Tursiops*) shows the same pattern; again, the animals in the open Atlantic are the largest and those in the Black Sea the smallest.

Another common pattern is larger size in inshore coastal

The extremely attenuated northern right whale dolphin, *Lissodelphis borealis*, lacks a dorsal fin and is sometimes called "snake porpoise" by fishermen.



The dwarf sperm whale, *Kogia simus*, has many of the highly derived features of the sperm whale, *Physeter macrocephalus*, but it is only 2–3 meters long.



Two forms of the common dolphin, *Delphinus delphis*, inhabit the coast of California. The pelagic form (top) is smaller and has a proportionately shorter beak than the neritic form (bottom). They also have different color patterns; note the width and position of the stripe running forward from the flipper.

populations than in more offshore populations. Two forms of the common dolphin, *Delphinus delphis*, inhabit the coastal waters of California. One is neritic and the other pelagic. The more inshore form is larger and has a larger skull than the more offshore one.

In a last example, spinner dolphins (*Stenella longirostris*) in the far eastern oceanic tropical Pacific are sharply different from those in other tropical oceans around the world. The spinner dolphins in the eastern tropical Pacific are all gray, and in the adult male the dorsal fin is canted forward. This unusual dorsal fin is correlated with a large ventral hump behind the anus. These spinners are found in areas of the eastern Pacific where the thermocline is steep and the mixed layer shallow, approximately 50–60 meters. The spinner dolphins in other tropical waters, for example around Hawaii, have a sharply defined three-part color pattern, a slightly falcate dorsal fin, and no ventral hump; this type is found in areas of deeper thermocline.

These two different forms used to be called separate species, but we now recognize them as subspecies. There is a broad zone of intergradation between them. The form endemic to the eastern Pacific is called the eastern spinner dolphin. The range of morphological variation here is much greater than is usually found in wild mammal species.

The major point about morphology in cetaceans is that diversity is as great or greater than in most terrestrial mammal groups. One just about has to go to the human species, or to domesticated animals, to find the degree of combined variation in size, coloration, and shape that exists in the spinner dolphin, for example.

We can safely say that the extensive geographical variation in cetaceans probably indicates that regional populations have been subjected to strong and diverse regional selection pressures, implying high habitat diversity within the major marine habitat types. The seas most definitely are not continuous in these terms. There is more diversity in the oceans than has been generally assumed, and therefore there are more kinds of animals, at and below the species level, that qualify as evolutionarily significant units that we should work to save.

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Geographic Variation in External Morphology of the Spinner Dolphin *Stenella longirostris* in the Eastern Pacific and Implications for Conservation

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Abstract. – Variation in color pattern, dorsal fin shape, and body length exhibit sharp north/south gradients centered at about 5–10°N latitude and east/west gradients at about 120–125°W longitude. A conservation zone with boundaries in these regions would provide protection for the morphologically unique eastern spinner dolphin *Stenella longirostris orientalis*. A radial pattern of geographic variation in the eastern Pacific and a complex pattern of discordant variation outside the core range of *S. l. orientalis* suggest that the present separate management of "whitebelly" spinner dolphins (which comprise a broad zone of hybridization/intergradation between *S. l. orientalis* to the east and the pantropical spinner dolphin *S. l. longirostris* to the west and southwest) north and south of the Equator may not be justified on the grounds of conservation of distinct populations.

Spinner dolphins in the eastern tropical Pacific vary geographically in color pattern (Perrin 1972), in external and skeletal size and shape (Perrin 1975, Perrin et al. 1979a, Schnell et al. 1982 and 1985, Douglas et al. 1986), and in reproductive seasonality (Barlow 1984). Perrin (1975) and Perrin et al. (1979a) described several forms that have served as stock units for management of populations of dolphins killed incidentally in the international purse-seine fishery for yellowfin tuna in the region (Perrin et al. 1985). Kills in recent years have been on the order of 100,000 annually. The management units have been known as the "Costa Rican," "eastern," "northern whitebelly," and "southern whitebelly" spinner dolphins. The geographic ranges of the eastern and whitebelly forms overlap broadly (Perrin et al. 1985).

The model used in studies and, to a lesser degree, management of the species in the region has been one of several discrete, more-or-less reproductively isolated stocks with some geographic overlap. However, as more morphological data have accumulated, a different picture has emerged. For example, while the boundary between the present northern and southern whitebelly management stocks was drawn latitudinally, the overall pattern of variation in the eastern Pacific now appears radial (Schnell et al. 1982 and 1985, Perrin et al. 1985). Further, the results of a genetic study indicate substantial exchange of at least mitochondrial DNA between and among the eastern and whitebelly forms (Dizon et al. 1991). Most recently, Perrin (1990) described two subspecies, *Stenella longirostris centroamericana* and *S. l. orientalis*, based on the Costa Rican and eastern forms, respectively, and concluded that the whitebelly "forms" (Fig. 1) collectively comprise a broad zone of intergradation or hybridization between the eastern subspecies and a third subspecies to the west and southwest, the pantropical spinner dolphin *S. l. longirostris*, a form occurring in the central and western Pacific, Indian and Atlantic Oceans (Perrin et al. 1981; Gilpatrick et al. 1987).

In this context, the purpose of the present study was to reexamine variation in external morphology on a finer geographical scale than had been used in earlier studies. Specimens previously identified as "Costa Rican," "eastern", or "whitebelly" based on the modal appearance of adult animals in the schools from which they came were pooled in the analyses. In this way we hoped to

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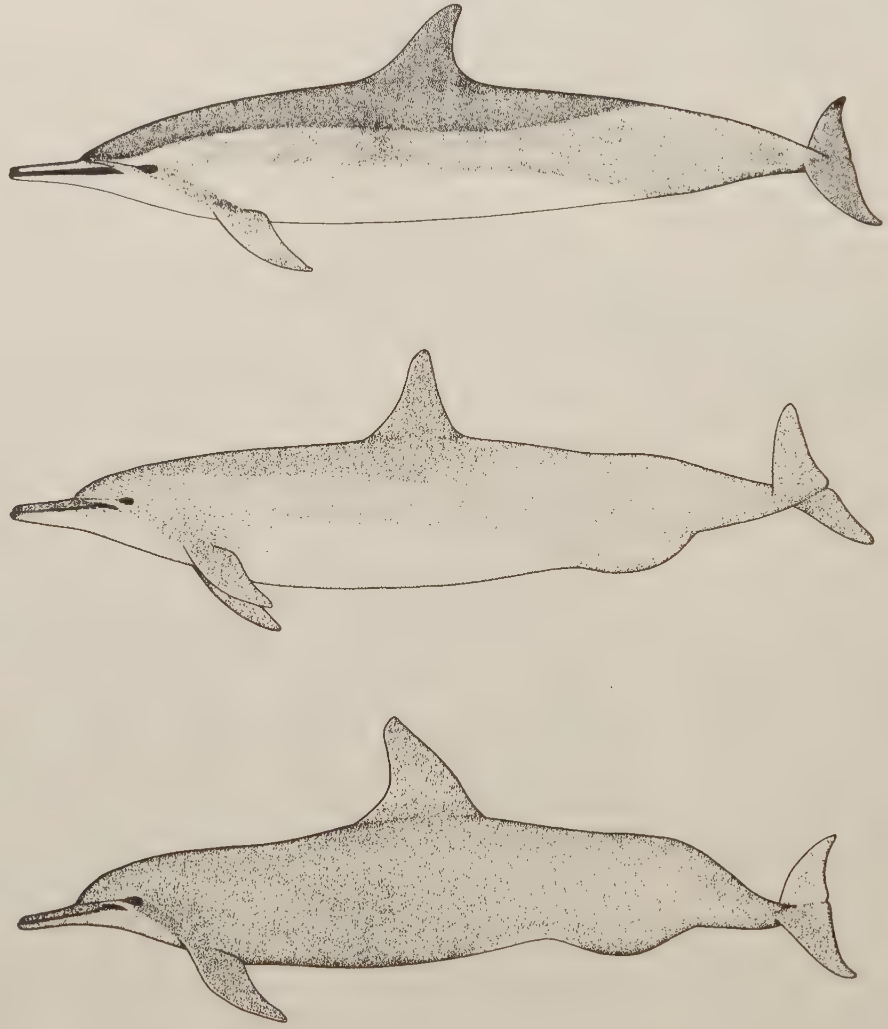


Figure 1
Typical appearance of adult males of the pantropical spinner dolphin *Stenella longirostris longirostris* (top), the eastern spinner dolphin *S. l. orientalis* (bottom), and a hybrid/intergrade "whitebelly spinner" (center).

gain a better understanding of the morphological gradients and other geographical patterning involved in the relationships among the Central American, eastern, and pantropical subspecies and to contribute to the development of approaches to conservation and management of the several populations.

Materials and methods

Source of the data

We examined variation in the ventral field and cape components of the color pattern (terminology of Perrin 1972), the shape of the dorsal fin, and body length.

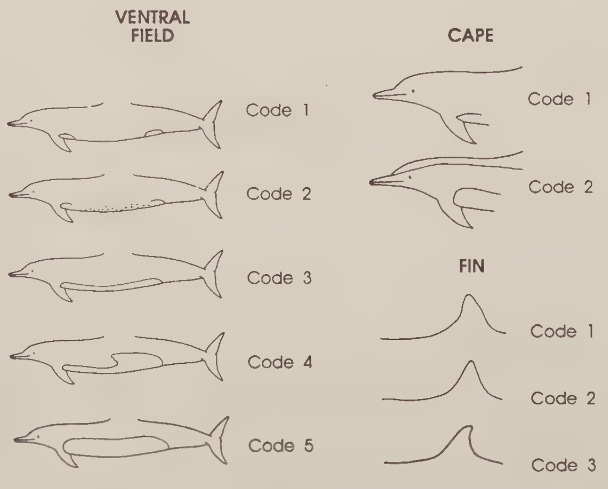


Figure 2

Character states for coding of ventral field, cape, and dorsal fin in spinner dolphins.

The data on color pattern and dorsal fin were collected by biologists during the period 1974–88 aboard commercial tuna seiners (see Acknowledgments). The length data were collected in 1968–89. The biologists completed a field "life-history" form for each dead dolphin examined, recording basic information such as sex and length and (starting in 1974) sketching in the ventral field, cape (if prominently visible; see below), and dorsal fin on a preprinted generalized dolphin outline. When feasible, the observer also traced the dorsal fin on the back of the data form. Body length was measured to the nearest cm with calipers mounted on a 2-m wooden ruler. For male specimens, a testis with epididymis attached was preserved and weighed ashore. For females, the number of corpora in the ovaries was determined in the laboratory (methods described in Perrin et al. 1976).

The quality of the sketches varied greatly. Although a few color pattern sketches were discarded as totally unusable, the basic features of the color pattern could be discerned in relatively inexpert sketches. However, the fin sketches proved to be unreliable. We found that for the cases where the observer both sketched and traced the dorsal fin, the correspondence between fin shape in the sketch and tracing was often poor. Therefore we used only the fin tracings, which reduced the sample size for dorsal fin shape. We also examined photographs of the specimens if they were available.

The analyzed data consisted of body length in cm and coded values for ventral field, cape, and dorsal fin shape. These were accompanied by date and location of capture and reproductive data (weight of testis + epididymis for males; number of ovarian corpora for females).

The ventral field received a code from 1 to 5 (Fig. 2). Code 1 is the state typical of the eastern subspecies; Code 5 is that typical of the pantropical subspecies (Fig. 1). Codes 2–4 are intermediate. In Code 1, the animal is gray laterally and ventrally, with white patches in genital and axillary regions. In Code 2, the separate genital and axillary white areas of Code 1 are joined by a speckled zone. In Code 3, the two areas are confluent, forming a white ventrum. In Code 4, the ventral field extends dorsally above the umbilical-genital region, yielding a stepped pattern in lateral view. In Code 5, the anterior portion of the ventral field extends dorsally to behind the eye, eliminating the step of Code 4. This variation is continuous, of course; a code was assigned for the state closest to that evident in the sketch. The sketches themselves already incorporated some artificial stratification. For example, in some animals the darker region yielding the step of Code 4 is only faintly evident. Some observers indicated the presence of this faint feature, leading us to code the animal as Code 4; others undoubtedly overlooked such faint markings or failed to record them, leading us to code the animals as Code 5. While such errors could be expected to blunt the resolving power of the analyses, there is no reason to suspect that they inject a systematic spatial bias that would affect the accuracy of the conclusions; the data were collected by a large number of observers working over large areas.

The cape (Fig. 2) was coded as "not noted in the sketch" (Code 1) or "noted in the sketch" (Code 2). In a living or freshly dead spinner dolphin, the cape can be discerned on close and careful inspection, if only very faintly, in all cases. In the eastern spinner, the dorsal overlay (terminology of Perrin 1972) is very dense, almost obliterating the underlying cape in even very fresh specimens. When a carcass of an eastern spinner has lain on the deck of a tuna boat for more than a few minutes, the dorsal overlay darkens to the point of completely obscuring the cape. In the live pantropical spinner, the dorsal overlay is less dense and the cape is sharply defined and obvious. It is detectable even in specimens dead for several hours, albeit more faintly. Thus the absence of the cape in a sketch means that the observer did not note it upon fairly cursory

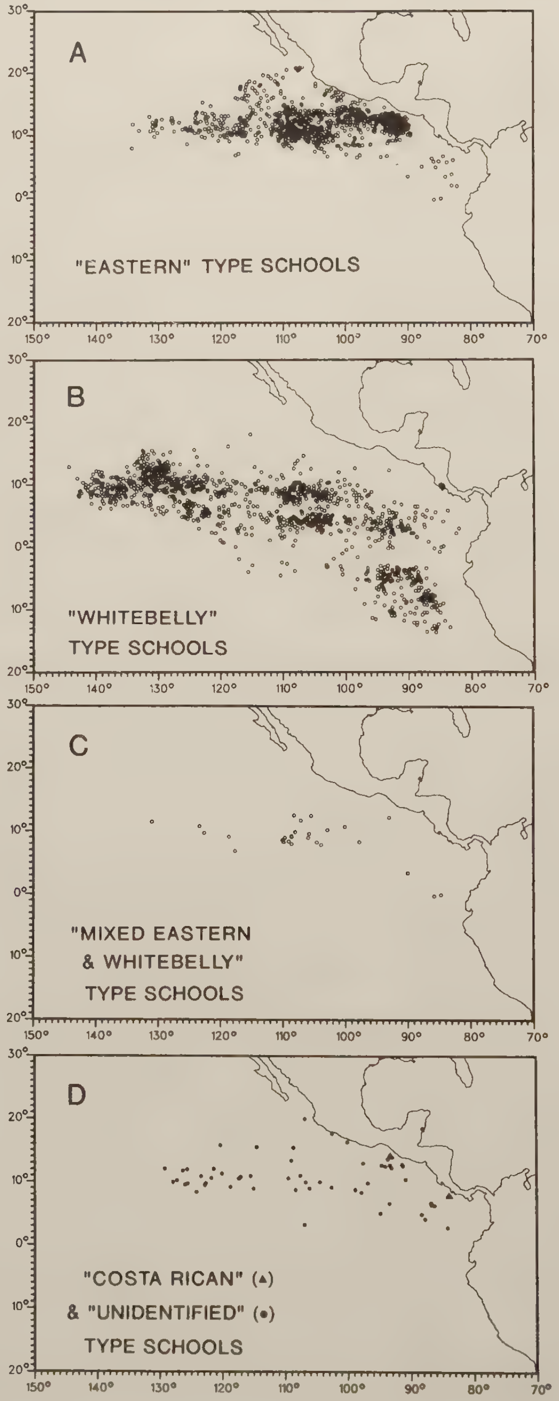

A
"EASTERN" TYPE SCHOOLS
B
"WHITEBELLY"
TYPE SCHOOLS
C
"MIXED EASTERN
& WHITEBELLY"
TYPE SCHOOLS
D
"COSTA RICAN" (▲)
& "UNIDENTIFIED" (●)
TYPE SCHOOLS
30°
20°
10°
0°
10°
20°
150°
140°
130°
120°
110°
100°
90°
80°
70°

Figure 3
Localities for purse-seine sets on schools of spinner dolphins for samples included in analyses, by school type (see text for school-identification criteria).

inspection, not that it was not actually absent. Cape "presence" is a relative measure of the density of the dorsal overlay, with some precision lost due to postmortem darkening. Again, under the assumption that time before examination of the carcasses and diligence of the observers did not vary with area, there should be no systematic bias.

The dorsal fin was coded to one of three states (Fig. 2): canted—closest to a right triangle with hypotenuse posterior (Code 1; most "eastern-like"), erect—isosceles triangle (Code 2), or falcate—right triangle with hypotenuse anterior (Code 3; most "pantropical-like"). Sources of error in this code include partial tracings of fins (part of the base of the fin not included) and injuries distorting the fin. The first was difficult to cope with and could not be resolved completely. Some tracings were discarded because of sharply anomalous shape obviously due to the fin being incomplete, but some small portion of the variation recorded is undoubtedly due to undetected errors of this sort. When a distal portion of the fin was missing due to injury, this was indicated in the observer's sketch, and the tracing was not used. The tracing was also not used if a very large notch or gap was indicated. Small notches and holes do not affect the overall shape of the fin.

The total of the code scores for the three characters ranged from 3 (typical of the adult male eastern spinner) to 10 (typical of the adult male pantropical spinner).

The sample

The sample for color pattern and fin shape included 8350 specimens from 971 net sets on "eastern"-type schools, 1200 sets on "whitebelly"-type schools, 27 sets on "mixed eastern and whitebelly" schools, 2 sets on "Costa Rican"-type schools, and 54 sets on spinner dolphins of unidentified stock (Figs. 3 and 4). Not all

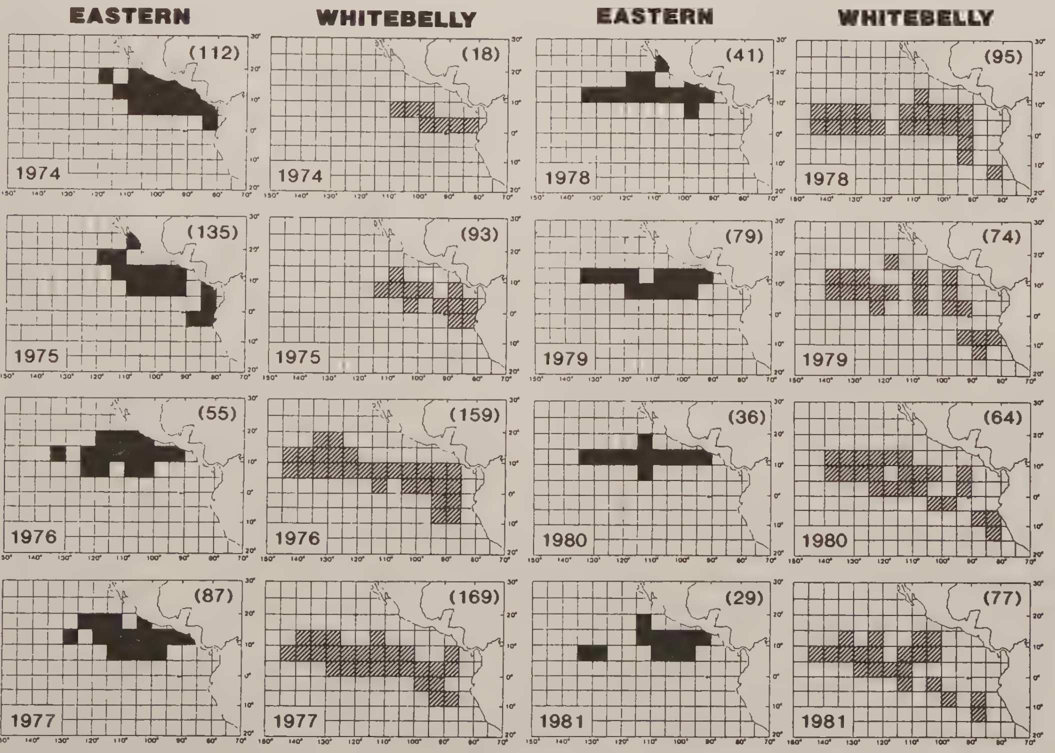


Figure 4
Distribution, by year, of purse-seine sets on "eastern" and "whitebelly" schools of spinner dolphins for samples included in analyses.

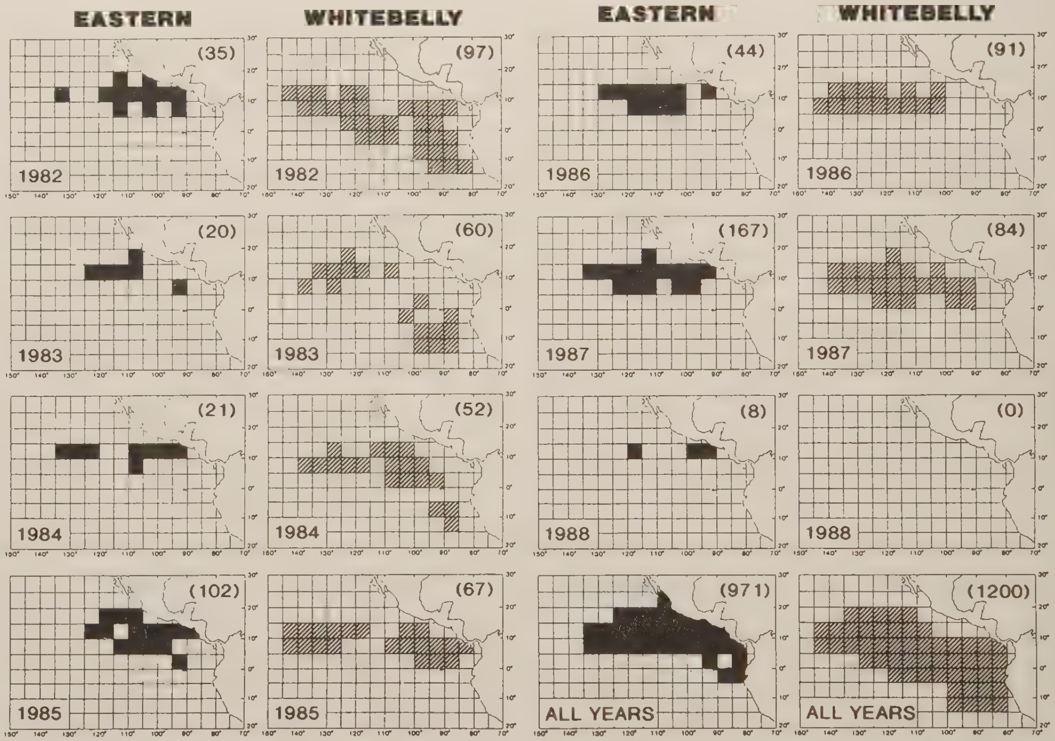

EASTERN
WHITEBELLY
EASTERN
WHITEBELLY
(35)
1982
(97)
1982
(44)
1986
(91)
1986
(20)
1983
(60)
1983
(167)
1987
(84)
1987
(21)
1984
(52)
1984
(8)
1988
(0)
1988
(102)
1985
(67)
1985
(971)
ALL YEARS
(1200)
ALL YEARS
30°
20°
10°
0°
10°
20°
150°
140°
130°
120°
110°
100°
90°
80°
70°

Figure 4 (continued)

of the characters were recorded for all of the specimens (Table 1). Body-length data were available for 3304 adult dolphins (1461 males and 1843 females). (Females with at least one ovarian corpus and males with testis/epididymis weight of 100g or more were considered adult, following Perrin et al. 1977.)

Analytical methods

Areal stratification For purposes of the analyses, we divided the study area into 60 5-degree blocks with boundaries at the Equator, 5 degrees, 10 degrees, etc., and 80 degrees, 85 degrees, etc. We experimented with 4-degree blocks and with different placement of the boundaries but obtained less consistent results (more embedded and peripheral anomalous blocks) than with the scheme adopted.

Effects of sexual dimorphism and development Color pattern and fin shape are known to vary with sex or age or both (Perrin 1972). We endeavored to take into account these factors in the geographical analyses by considering males and females separately where necessary and by applying a minimum length or sexual-maturity criterion for specimens to be included in analyses of each of the characters separately.

Table 1
Sample sizes for analyses of color pattern and fin shape of spinner dolphin in the eastern tropical Pacific Ocean.

Character	Males	Females	Total
Total individuals	4121	4229	8350
Ventral field	3377	3463	6840
Cape	3376	3462	6838
Fin shape	2053	2421	4474
Adults with all 3 characters	610	683	1239

Because they relate primarily to the methodology of the study, the results of analyses to establish the length/maturity criteria are presented here rather than below with the results of the analyses of geographical variation.

We found no difference between the sexes in extent of the ventral field but a statistically significant association between ventral field state and body length (contingency test of association with Peterson's chi-square, α 0.05; computer program BMDP4F in Dixon et al. 1990). As described by Perrin (1972), all calves tend toward the "whitebelly" color pattern (codes 4 or 5), with reduction in the ventral field in "eastern" spinners with age (to Codes 1, 2, or 3). The proportion in the overall present sample with Code-5 ventral field (most "whitebelly-like") declined with body length until about 120 cm, when it stabilized at about 30–35% (Fig. 5), and the proportion of individuals with Code 1 ventral field (most "eastern-like") behaved similarly but conversely. We therefore limited the analyses of ventral field to specimens of 120 cm or larger. (After about 170 cm, the proportion of Code-5 animals again climbed and Code-1 animals decreased; this is because most specimens above that length were "whitebelly" spinners—see analyses below of geographical variation in body length.)

Noted presence of the cape exhibited a similar pattern of change with growth (Fig. 6). Calves in all regions tend to exhibit a strongly defined cape, which is progressively obscured with development of the "eastern" pattern (Perrin 1972). Again, relative stability in the proportion of all animals for which the cape was noted was reached at about 120 cm in both sexes; the sample for the geographic analyses was limited to specimens of this length or greater.

We also found a slight association of expression of the cape with gender; the cape was noted for 10.1% of all females but only 7.8% of males (Fig. 6). In the geographical analyses, we used the average of male and female means in order to avoid effects of possible areal variation in sex ratio in the samples.

The degree of sexual dimorphism in the shape of the dorsal fin varies geographically, ontogenetically, and individually (Perrin 1972). In the present sample, in schools classified as "eastern" (Fig. 7), about 60% of small calves of both sexes had erect dorsal fins (Code 2); the balance had falcate fins (Code 3). Beginning at about 135 cm, erect fins increasingly predominated, to more than 80% in large juveniles of both sexes and about 90% in adult females. In males, the first canted fins (Code 1) appeared at about 160 cm. They increased in frequency to about 70% in large adults of 180 cm or more. This corresponds roughly to the length at which about 80% (the asymptotic level) have achieved at least minimum testis-epididymis weight (94 g) at which spermatogenesis occurs (Perrin and Henderson 1984). Thus, the canted fin in the eastern-type animals was strongly associated with sexual maturity, although some mature males had erect fins.

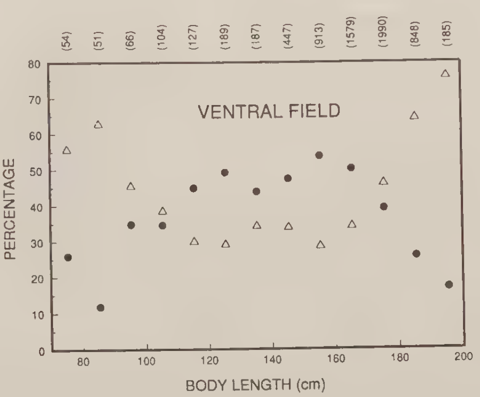


Figure 5

Change in ventral field in relation to body length in spinner dolphins. Circles are Code 1; triangles are Code 5. All specimens over 195 cm included in last interval. Sample sizes in parentheses (total 6840).

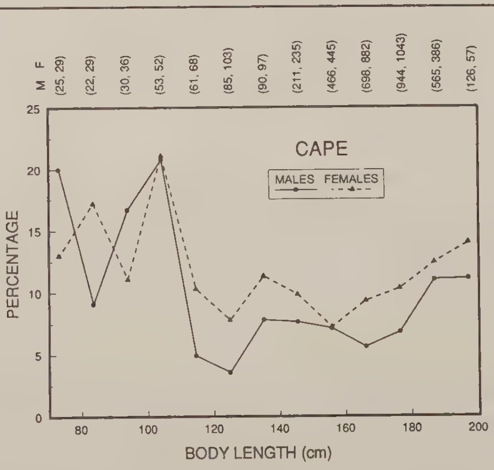


Figure 6

Change in percentage with noted cape in relation to body length in males and females. All specimens over 195 cm included in last interval. Sample sizes in parentheses (total males 3376, total females 3462).

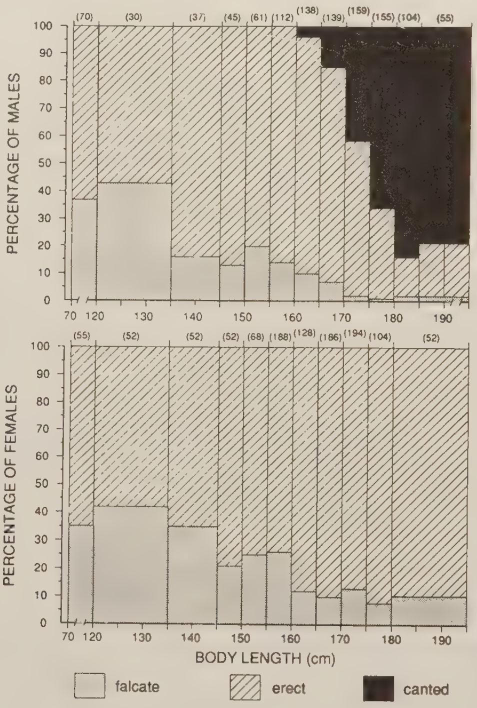


Figure 7

Change in percentage of males (top) and females (bottom) from "eastern"-type schools with canted (Code 1), erect (Code 2), and falcate (Code 3) dorsal fins in relation to body length. Sample sizes in parentheses.

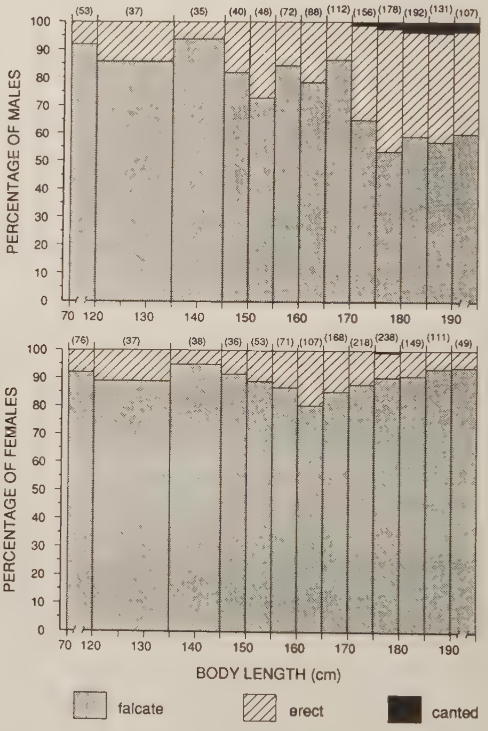


Figure 8

Change in percentage of males (top) and females (bottom) from "whitebelly"-type schools with canted (Code 1), erect (Code 2), and falcate (Code 3) dorsal fins in relation to body length. Sample sizes in parentheses.

In the "whitebelly" schools (Fig. 8), roughly 90% of calves, juveniles, and adult females had falcate dorsal fins and about 10% erect fins. One adult female had a canted fin. In adult males, the frequency of erect fins increased to about 40% in individuals of 175 cm or more (2.3% had canted fins). Again, this is about the length at attainment of sexual maturity (*loc. cit.*). We limited the analyses of dorsal fin shape in the pooled samples to sexually mature dolphins and considered males and females separately.

We followed the same procedure for analyses of body length, limiting the sample to sexually mature animals and analyzing males and females separately.

Effects of seasonal variation The apparent overlap of collection localities for the two kinds of schools is not an artifact of seasonal migrations. The region of substantive overlap of "eastern" and "whitebelly" schools is between 8° and 12°N and 95° and 125°W (Fig. 3). We examined the data by quarter of the year and found overlap in this region in all four quarters.

Pooling to obtain adequate sample sizes Sample sizes in many cases were very small for some of the peripheral 5-degree blocks. In these cases we pooled the samples over two or more blocks, to achieve a minimum sample size of 25. In the pooling we attempted to approximate the apparent radial pattern of variation, i.e., pooling was mainly longitudinal in the south and mainly latitudinal in the west. To the extent possible, we maintained the same pooling scheme from analysis to analysis, although in some cases differential pooling was required for males and females. The sample sizes and pooling schemes for the various analyses are given in the Appendix.

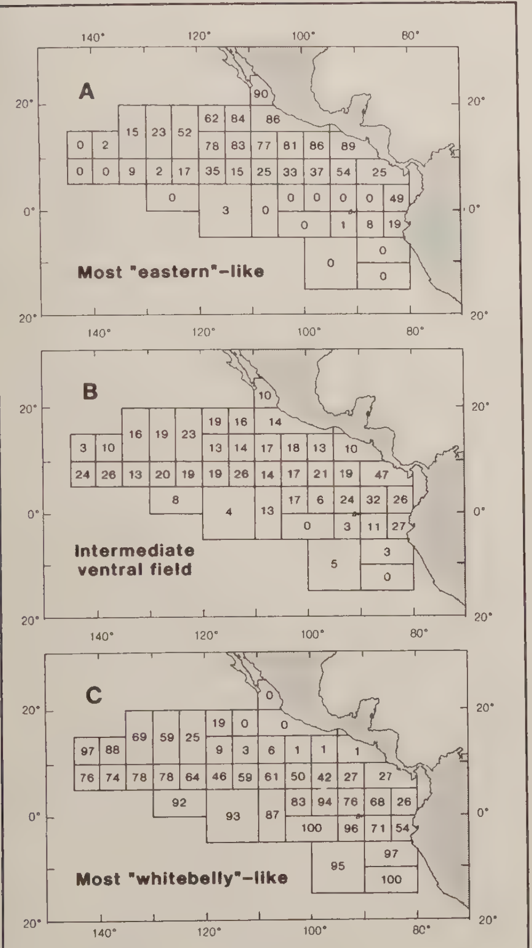

A
90
62 84 86
15 23 52
0 2
78 83 77 81 86 89
0 0 9 2 17 35 15 25 33 37 54 25
0
0 0 0 0 49
3 0
0 1 8 19
0
0 0
Most "eastern"-like
B
10
19 16 14
16 19 23
3 10
13 14 17 18 13 10
24 26 13 20 19 19 26 14 17 21 19 47
8
17 6 24 32 26
4 13
0 3 11 27
3
5
0
Intermediate ventral field
C
0
19 0 0
69 59 25
97 88
9 3 6 1 1 1
76 74 78 78 64 46 59 61 50 42 27 27
92
83 94 76 68 26
93 87
100 96 71 54
97
95
100
Most "whitebelly"-like
140° 120° 100° 80°
20° 0° 20°

Figure 9

Percentage of spinner dolphins exhibiting (A) Code 1 (most "eastern-like"), (B) Codes 2, 3, and 4 (intermediate), and (C) Code 5 (most "whitebelly-like") ventral fields, by area.

Contouring We used the ZSMTH, ZGRID, and ZCSEG subroutines of the PLOT88 graphics software package (Young and Van Woert 1987) to generate contours of ventral coloration scores for unweighted 5-degree blocks. The center of a block was used as the position for the mean ventral coloration score of specimens collected within the block. We used ZGRID with the "cay" parameter set at 5 and "nrng" set at 4 to generate a data grid for contouring. ZSMTH with "nsm" set at 1 was used to smooth the grid. Contour lines were generated using ZCSEG with "ndiv" set at 4.

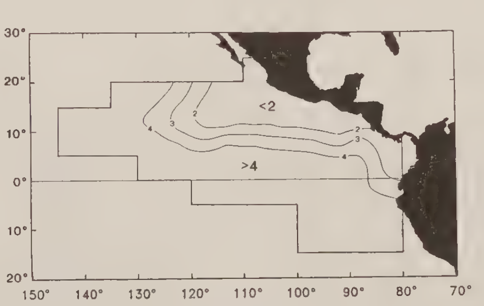

<2
>4
2
3
4
30° 20° 10° 0° 10° 20°
150° 140° 130° 120° 110° 100° 90° 80° 70°

Figure 10

Contours of ventral-field codes for spinner dolphins ⩾120 cm. Based on 5-degree block averages (see text).

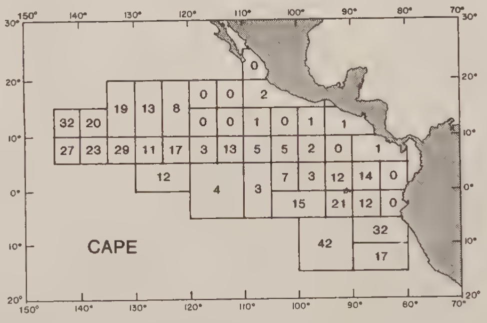

0
0 0 2
19 13 8
32 20
0 0 1 0 1 1
27 23 29 11 17 3 13 5 5 2 0 1
12
7 3 12 14 0
4 3
15 21 12 0
32
42
17
CAPE
150° 140° 130° 120° 110° 100° 90° 80° 70°
30° 20° 10° 0° 10° 20°

Figure 11

Percentage of spinner dolphins with observed cape, by area.

Results

Ventral field

The pattern of disjunct axillary and genital white areas (Code 1) occurred at high frequencies (⩾75%) in a relatively small part of the study area, in 12 5-degree blocks north of 10°N and east of 120°W (Fig. 9A). It was totally absent south of 5°S and absent from most of the peripheral blocks between 15°N and 5°S. It occurred at intermediate frequencies near Central America and northern South America, between 10°N and 5°S. The steepest gradient would appear to have been at about 10°N, extending from the coast out to possibly beyond 125°W. This pattern was mirrored in the relative distribution of the Code-5 ventral field (most "whitebelly-like"), which was absent or nearly absent from most of the northeastern blocks where the Code 1 pattern predominated and occurred at frequen-

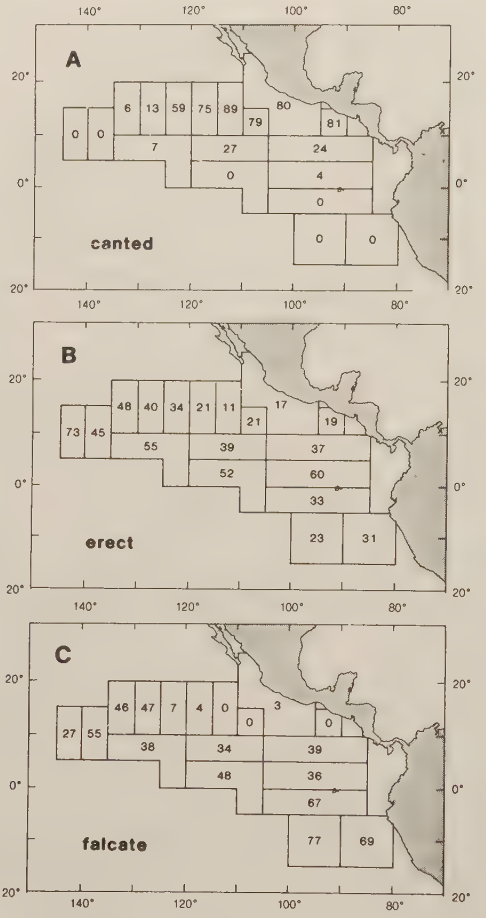


Figure 12
Percentages of adult male spinner dolphins with (A) canted, (B) erect, and (C) falcate dorsal fins, by area.

cies above 75% in a broad band encompassing the study area south of 15°N (Fig. 9C). Again, *per force*, the steepest gradient was at about 10°N.

Dolphins with intermediate ventral fields (Codes 2–4) were least frequent in the peripheral blocks to the south and southwest and most frequent in a region off Central America below 10°N (Fig. 9B).

Contouring of the ventral-field data based on 5-degree block averages (Fig. 10) yields a clear pattern of extensive, largely Code-1 and Code-5 regions divided by a steep gradient.

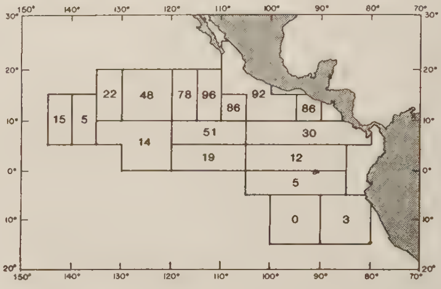


Figure 13
Percentage of adult female spinner dolphins with erect dorsal fins, by area. Of remaining, one had canted fin, others had falcate fins.

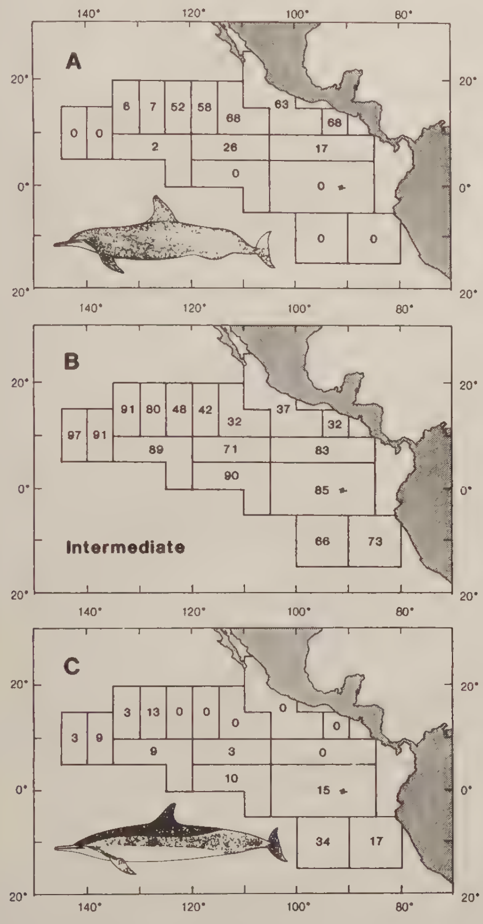
Cape

The percentage of dolphins with observed cape was highest in the far south and far west (Fig. 11). This pattern differs from that for the ventral field. For the ventral field (Fig. 9C), the zone of high frequency of Code-5 fields was continuous along a southeast-northwest axis, whereas for the cape the two regions of relatively high frequency in the south and north were separated by a broad zone of relatively low frequency. In addition, the north–south gradient in expression of the cape was not as steep (at 10°N) as for the ventral field.

Dorsal fin

Because of sexual dimorphism and the need to restrict the analyses to sexually mature animals, sample sizes were very much smaller for this character than for the cape and ventral field, necessitating more extensive pooling. Parts of the areas off northern South America and in the southwestern portion of the study area that were included in the coverage for the color pattern characters are not covered in the fin samples.

Despite the reduced resolution in the analyses of dorsal fin variation, some patterns are evident (Figs. 12, 13). In the males the sharp gradient at about 10°N (Figs. 12A, C) is concordant with the pattern for the ventral field (Fig. 9); the canted fin, like the disjunct ventral field, occurred at high frequency (≥75%) only in a region bounded approximately by 10°N and 120°W. The same is true of the erect fin in the female (Fig. 13). The falcate fin in males was more common south of the Equator; 90 of 127 males (71%) in the three southernmost cells that contained no males with canted fins had falcate fins, but only 25 of 66 (44%) in the


140°
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A
0 0 6 7 52 58 68 63 68
2 26 17
0 0
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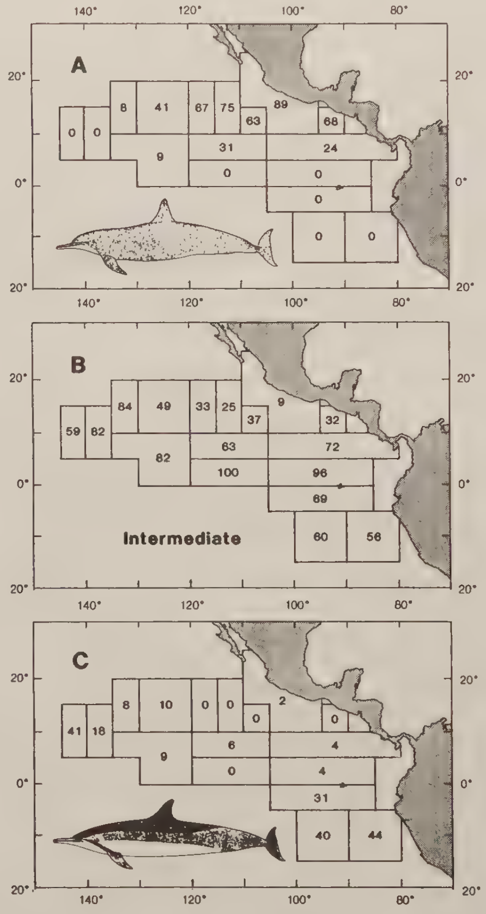
B
97 91 91 80 48 42 32 37 32
89 71 83
90 85
66 73
Intermediate
C
3 9 3 13 0 0 0 0 0
9 3 0
10 15
34 17

Figure 14
Percentages of adult male spinner dolphins having most "eastern" (A), most pantropical/"whitebelly" (C), and intermediate combinations (B) of ventral field, cape, and dorsal fin, by area.


140°
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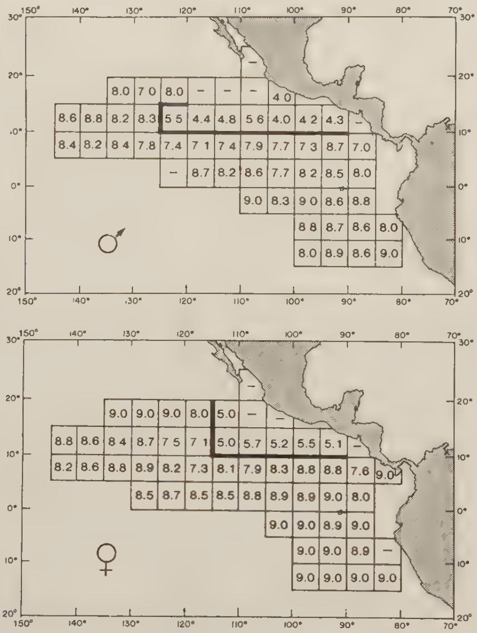
A
0 0 8 41 67 75 63 89 68
9 31 24
0 0
0
0 0
B
59 82 84 49 33 25 37 9 32
82 63 72
100 96
69
60 56
Intermediate
C
41 18 8 10 0 0 0 2 0
9 6 4
0 4
31
40 44

Figure 15
Percentages of adult female spinner dolphins having most "eastern"-type (A), most pantropical/"whitebelly"-type (C), and intermediate combinations (B) of ventral field, cape, and dorsal fin, by area.

two westernmost cells had falcate fins. This difference is statistically significant ($P<0.0001$: Fisher's exact test, two-tailed). The frequency of falcate fins in the two southwestern cells between 10°N and 5°S was intermediate (Fig. 12B). In females, the falcate fin was also most common in the south, although in this case the frequency there was not statistically different from that in the two westernmost cells at $P=0.05$.

Combined characters

Data on all three characters (ventral field, cape and dorsal fin) were available for 610 sexually adult males and 683 females. The distributions of the extreme expression of eastern character combinations (a total score of 3 for males and 4 for females) and pantropical combinations (10 for both males and females) were similar for males and females (Figs. 14, 15). Only the extreme eastern combination predominated (more than 50%) in any area, in a region bounded by 10°N and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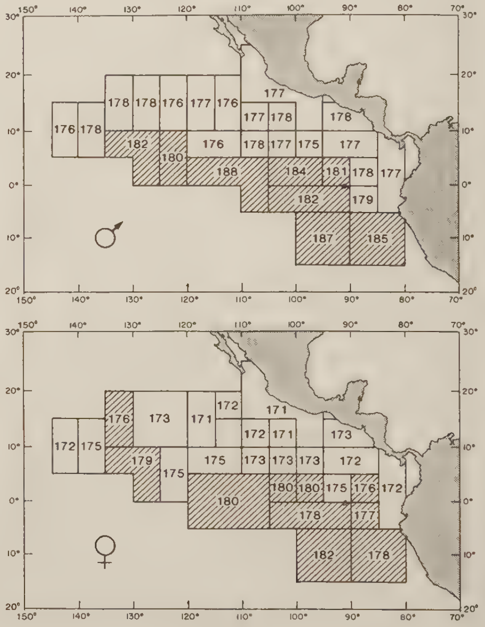
8.0 7 0 8.0 – – – 4 0 –
8.6 8.8 8.2 8.3 5 5 4.4 4.8 5 6 4.0 4 2 4.3 –
8.4 8.2 8 4 7.8 7.4 7 1 7 4 7.9 7.7 7 3 8.7 7.0
– 8.7 8.2 8.6 7.7 8 2 8.5 8.0
9.0 8.3 9 0 8.6 8.8
8 8 8.7 8.6 8.0
8.0 8.9 8.6 9.0
♀
9.0 9.0 9.0 8.0 5.0 – – –
8.8 8.6 8 4 8.7 7 5 7 1 5.0 5.7 5.2 5.5 5.1 –
8.2 8.6 8.8 8.9 8.2 7.3 8.1 7.9 8.3 8.8 8.8 7.6 9.0
8.5 8.7 8.5 8.5 8.8 8.9 8.9 9.0 8.0
9.0 9.0 8.9 9.0
9.0 9.0 8.9 –
9.0 9.0 9.0 9.0

Figure 16

Average combined score for spinner dolphins with intermediate combinations (see Figure 19) of ventral field, cape, and dorsal fin, by 5-degree block (no pooling). Heavy line is between blocks with average score ≥7.0 and those with score <6.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176 178 177 178 178
182 180 176 178 177 175 177
188 184 181 178 177
182 179
187 185
♀
176 173 171 172 171
172 175 172 171 173
179 175 175 173 173 173 172
180 180 180 175 176 172
178 177
182 178

Figure 17

Average body length of adult male and female spinner dolphins, by area. For males, cells with length ≥180 cm are hatched; for females, cells with length ≥176 cm are hatched (adult males are about 4 cm longer than adult females on average; Perrin et al. 1985 and present data).

125°W for males (Fig. 14A) and 10°N and 120°W for females (Fig. 15A). It was absent in the cells south of 5°N and east of 120°W and in the cells west of 135°W. The extreme pantropical combination reached only 34% in males, in the southernmost region (Fig. 14C), and 44% in females (Fig. 15C). It was absent (except for one female) from the cells in which the eastern combination predominated (north of 10°N and east of 120–125°W). It was present only at low levels in the southwestern region, about the same as just to the south and west of the core eastern region. Except in the core eastern region, the majority of dolphins were intermediate (combined scores of 4–9 for males and 5–9 for females (Figs. 14B, 15B); in some cells between 0° and 15°N, over 95% of the adults were intermediate. Even in the core eastern region, about one third were intermediate. The degree of intermediacy was not uniform, however. For both sexes, there was a very steep latitudinal gradient in average scores of intermediate animals at about 10°N (Fig. 16). There was also a steep longitudinal gradient, at about 125°W for males and 115°W for females. Outside this sharply bounded core "eastern" region, variation in intermediate scores was very much less, with only slight N/S and E/W gradients and most animals relatively close to the pantropical extreme.

Proportionately more adult females than adult males in the westernmost cells (west of 140°W) were of the extreme pantropical combination (Fisher's exact test, $P<0.01$), whereas this was not as true in the southernmost cells ($P>0.10$).

Body length

The major shift in average adult length of both males and females (Fig. 17) was at about 5°N, rather than at about 10°N as for the other characters (e.g., compare with Figs. 14–16). The region of smaller animals extended south along the coast of northern South America to about 5°S. Animals from the far west were

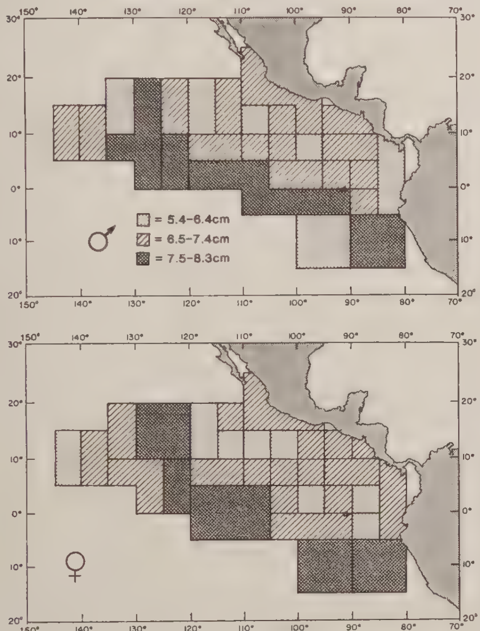


Figure 18
Standard deviations (in cm) of body length for adult male and female spinner dolphins, by area.

Table 2
Variability of body length in sexually adult spinner dolphins of eastern (combined scores of 3 for males or 4 for females) and pantropical (combined score of 10 for both males and females) morphology (ventral field, cape, and dorsal fin) from the eastern Pacific.

	Eastern		Pantropical	
	Males	Females	Males	Females
Sample size	136	195	47	78
Average length (cm)	178.9	172.7	181.9	177.2
SD (cm)	6.30	5.90	7.46	7.84
CV	3.52	3.42	4.10	4.43

more closely associated in average length with those in the east than those in the far south (below 5°S).

Body length is more variable in the regions of greater body length, in both males and females (compare Figures 17 and 18; Table 2).

Discussion

Year-to-year variation and home range

The patterns of distribution of the eastern spinner and the "whitebelly" intergrades/hybrids appear to be relatively stable year to year, although analysis of the present data is complicated by the fact that they come from incidental kills in a very mobile pelagic tuna fishery. The cumulative maps of specimen localities (Figs. 3, 4) show the locations where tuna boats made purse-seine sets that killed spinner dolphins. It reflects only co-occurrence of tuna boats, spinner dolphins, and yellowfin tuna. In addition, the spinner dolphin is not the main target dolphin species in the fishery; the pantropical spotted dolphin *Stenella attenuata* is relatively more often found together with tuna. The sets on spinner dolphins are largely sets on mixed schools of spotted and spinner dolphins; in some areas, especially in the southern and southwestern regions of the study area, spinner dolphins are not often associated with spotted dolphins and seldom are with tuna (Au and Perryman 1985).

Not all regions represented by capture localities in the cumulative maps (Fig. 3) are represented in the maps for individual years (Fig. 4). Possible reasons for this are (1) the dolphins moved around from year to year, (2) the tuna vessels moved around, (3) the yellowfin tuna moved around, and, most likely, (4) some combination of (1), (2), and (3). For some years (e.g., 1985–87), the samples included no spinner dolphins from south of the Equator, but dolphin research survey cruises in that region in 1986 and 1987 made numerous sightings (Holt and Jackson 1987, 1988). That particular hiatus in the maps of localities for at least some years therefore represents the absence of tuna vessels and possibly yellowfin tuna associated with dolphins, not an absence of spinner dolphins. On the other hand, the pattern of paired latitudinal bands of high density of localities for "whitebelly" schools in the cumulative map (Fig. 3) was not apparent in annual plots. It resulted mainly from relatively large numbers of specimens from the area of the upper band in 1975 and 1984–87 and from the lower band in 1977 and 1978. "Eastern" schools were sampled from the region of the northern band in all years. Again, research surveys in 1986 and 1987 sighted comparable numbers of "whitebelly" spinner schools in the two regions. In this case, it is possible that the pattern or degree of association of tuna with the two forms varied interannually. However, the numbers of sightings of spinner dolphins during all the research cruises were relatively small, and it remains possible that some portion of the patterning in the cumulative distribution represents interannual variation in distribution; i.e., the northern boundary of the main "whitebelly" distribution may fluctuate year to year by about 5 degrees of latitude. This would be consistent with some of the results of the present study; for example, the intermediate percentages of the extreme "eastern" and "whitebelly" character states in the band between 5° and 10°N (Figs. 9–10, 12–15).

Another possible explanation of the latitudinal pattern has to do with distribution of tuna-fishing effort. During the period 1976–79, the Inter-American Tropical Tuna Commission set a regulatory demarcation line at 5°N, between 95° and 110°W. During this period, when an annual areal quota of yellowfin tuna for the region north of the line was filled, the international fleet was forced to fish south of the line or to the west (Peterson and Bayliff 1985). A similar line was in force in 1973–75 at 3°N. The subsidiary latitudinal band of distribution records south of 5°N apparent in the spinner dolphin data is also present in data for the pantropical spotted dolphin *S. attenuata*, the principal target species of the tuna fishery (Perrin et al. 1983). Illustrations of the effect of the regulatory regime on the distribution of fishing effort are given in Punsley (1983); the effect was particularly pronounced in 1978.

Some of the morphological results speak against the hypothesis of large-scale latitudinal movements. Variation among sub-areas of the "whitebelly" range is discordant. For example, for the character "ventral field" (Figs. 9, 10), the far-western blocks, far-southern blocks, and southwestern blocks are similar in having relatively high frequencies of the Code-5 character state (most "whitebelly-like"), while for the "cape" (Fig. 11), the southwestern region differed from the west and south in having low frequencies of observed cape (they were most like the animals immediately to the north). For male/female dorsal fin shape (Figs. 12, 13), the southern blocks had higher frequencies of the falcate fin than did the western blocks. While in color pattern and in cranial characters (Schnell et al. 1985), the westernmost blocks were most like the southern blocks, in body length and variability of body length (Figs. 17, 18) they were most like the northern and central blocks. The blocks just north of the Equator were remarkable in having very high frequencies of females intermediate between the most "whitebelly" state and the most "eastern" state in combined character scores (Fig. 15); the highest frequencies of these in males were in the westernmost blocks. In body length in both males and females (Fig. 17), the steepest gradient was at about 5°N, whereas in combined ventral field, cape and dorsal fin (Figs. 14, 15), it was at about 10°N. In cape (Fig. 11) and body length (Fig. 17), the dolphins in the Panama Bight and just to the south were most like those in the core "eastern" region (lacking visible cape and small in body size), but in ventral field (Fig. 9) they were intermediate between those to the north and south, having approximately equal frequencies of Code 1, Code 5, and summed Codes 2–4. This complex patchwork of variation suggests that there is not a large amount of movement between the various regions and that the year-to-year variation in the collection localities (Figs. 3, 4) reflects mainly movements of the tuna vessels and perhaps the tuna.

The complex geographical pattern of variation in the zone of intergradation/hybridization ("whitebelly spinners") is consistent with the limited information from tag returns (Perrin et al. 1979b), which suggests a home range of a diameter of hundreds rather than thousands of kilometers. This is also supported by the stability of the core eastern region between years and patterns of reproductive seasonality that suggest areal structure within the eastern region (Barlow 1984).

However, there may be mid-scale seasonal movements within an overall pattern of interannual stability, especially in the "whitebelly" areas outside the core range of the eastern spinner. Based on census surveys from dedicated research vessels, Reilly (1990) reported increases in abundance west of 120°W along 10°N coincident with seasonal shoaling of a thermocline ridge. Because of interannual variation in distribution of tuna fishing effort (discussed above), the coarse geographic strata used, and the relatively small sample sizes for the outlying strata, the present analyses probably could not be expected to detect such shifts, although the shifts might be expected to blur the perceived patterns of morphological gradients.

Taxonomic status and management of the "whitebelly" spinner dolphin

The "whitebelly" spinner has been managed as two "stocks" divided at the Equator, the northern whitebelly spinner and the southern whitebelly spinner, implying effective reproductive isolation between them and from the eastern spinner (e.g., Hall and Boyer 1990). The complex pattern of discordant geographic variation and the relatively higher standard deviations (of body length) in the range of the "whitebelly" spinner are typical of a hybrid zone resulting from what Mayr (1970) called allopatric hybridization, or "the formation of a secondary zone of contact and of partial interbreeding between two formerly isolated populations that had failed to acquire complete reproduction isolation during the preceding period of geographic isolation." The discordant pattern speaks against the earlier hypothesis of a locally adapted "whitebelly" population sharing features with populations to the east and west and defined by morphological clines. An hypothesis of secondary contact after isolation (Perrin et al. 1985) and consideration of the patterns of variation led to the formal recognition of the eastern form as a subspecies, *Stenella longirostris orientalis*, and the "whitebelly" form as an hybrid/intergrade between that subspecies and the pantropical spinner dolphin *S. l. longirostris* (Perrin 1990). The hypothesis of genetic exchange between the eastern and "whitebelly" populations is also supported by results of analysis of mitochondrial DNA (Dizon et al. 1991); the presence of unique haplotypes that would be expected in isolated populations was not detected. Given this situation, a relatively higher priority should probably be given to protection of the eastern subspecies on the grounds that it is a distinctly and locally adapted form vulnerable to depletion and to genetic "swamping" from the larger and less-exploited population to the west. In any case, the understanding presented here of the complex pattern of variation within the "whitebelly" range does not support the present division into northern and southern stocks for management on grounds of population distinctness.

Conservation and management of the eastern spinner dolphin

There was generally good concordance between the patterns in the individual morphological characters and the relative distributions of the two kinds of schools as identified by modal appearance (Fig. 3). One exception was the region west of the Bight of Panama; here the very high frequency of morphologically intermediate dolphins and virtual absence of animals of the extreme "eastern" appearance indicate that these schools perhaps would have better been identified as "whitebelly" schools. Apart from this discrepancy, the concordance between the character patterns and the field identification of schools suggests that the modal-appearance method of identification is largely effective. The substantial number of "mixed schools" and unidentified schools, however, indicates that the method can still offer difficulties. In addition, it is sometimes difficult to identify a school of spinner dolphins to "stock" (eastern or "whitebelly") before the seine is set. This can be due to poor viewing conditions (time of day, angle of sun, amount of wind, height of swell) or to the behavior of the dolphins (e.g., "laying low," precluding observation of ventral coloration).

An alternative management scheme based on geographic location would avoid the difficulties of field identification of schools. Although the working hypothesis for management of the eastern spinner and the "whitebelly" spinner (eastern/pantropical hybrids or intergrades) has been one of broadly overlapping ranges (e.g., Perrin et al. 1985), the actual transition between the two as indicated by gradients in the morphological characters and the field identifications (Fig. 3) is quite sharp. An "eastern spinner conservation zone" could be devised that would offer appropriate and unequivocal protection to the unique and coherent gene pool of the eastern subspecies. For example, such a zone bounded by 10°N latitude and 125°W longitude, the approximate latitude and longitude of the major gradients in the morphological characters, would have included 84% of the schools identified in the field as "eastern" (excluding those in the Bight of Panama, discussed above) and only about 5% of those identified as "whitebelly" (Fig. 19). Implementation of an international quota or prohibition for such a zone would be straightforward. The boundaries could be set based on a balance of considerations of conservation and operational practicality and should take into account seasonal and interannual variation in locations of concentrations of schools of the eastern spinner.

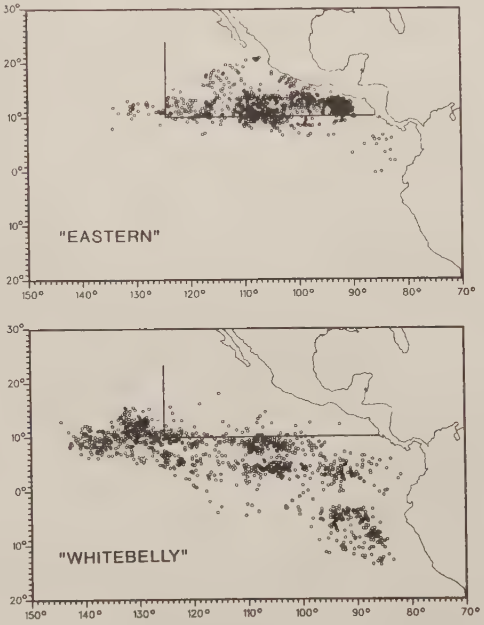


Figure 19
Localities of "eastern" and "whitebelly" schools of spinner dolphins included in the present analyses in relation to an example of a possible conservation zone for the eastern subspecies, *Stenella longirostris orientalis*.

This scheme, of course, is only one of numerous possible alternatives to conservation and management of the subspecies. Others include international application of a stock quota, complete bans on this type of fishing, and increased focus on technological efforts to reduce fishing mortality rates, to name a few.

The Central American spinner ("Costa Rican spinner")

The number of "Costa Rican" schools sampled was too small for meaningful separate analysis (2 of 1454; Fig. 3) and the effect on the analyses of including them in the pooled samples can be considered negligible. In any case, the range of the Central American spinner *S. l. centroamericana* as presently understood (a coastal strip about 50 nmi wide between about 13° and 7°N) does not overlap those of the eastern subspecies or the "whitebelly" hybrid/intergrade forms (Perrin 1990). This range could serve as a management unit for the subspecies.

Acknowledgments

The data used in this study were collected by biological technicians aboard commercial tuna seiners. We wish to thank these people and the captains and crews of the seiners; the research would have been impossible without their efforts and support. The sampling programs were supported by the U.S. National Marine Fisheries Service and the Inter-American Tropical Tuna Commission; both agencies gave us full access to data and specimens. R.B. Miller and others processed reproductive samples to determine sexual maturity. K.E. Wallace and R. Rassmussen provided data extraction services. R.C. Holland gave invaluable assistance with the contouring. J. Barlow carried out the Fisher's exact tests. R.M. Allen drafted the figures. J. Barlow, M. Scott, A.E. Dizon, I. Barrett, and S.B. Reilly reviewed the manuscript and offered many useful suggestions.

Citations

Au, D.W.K., and W.L. Perryman
1985 Dolphin habitats in the eastern tropical Pacific. Fish. Bull., U.S. 83:623–643.

Barlow, J.
1984 Reproductive seasonality in pelagic dolphins (*Stenella spp.*): Implications for measuring rates. Rep. Int. Whaling Comm. Spec. Issue 6:191–198.

Dixon, W.J., M.B. Brown, L. Engelman, and R.I. Jennrich (editors)
1990 BMDP statistical software manual, vol. 1. Univ. Calif., Berkeley, 629 p.

Dizon, A.E., S.O. Southern, and W.F. Perrin
1991 Molecular analysis of mtDNA types in exploited populations of spinner dolphins (*Stenella longirostris*). *In* Hoelzel, A.R. (ed.) Genetic ecology of whales and dolphins, p. 183–202. Rep. Int. Whaling Comm. Spec. Issue 13.

Douglas, M.E., G.D. Schnell, and D.J. Hough
1986 Variation in spinner dolphins (*Stenella longirostris*) from the eastern tropical Pacific Ocean: Sexual dimorphism in cranial morphology. J. Mammal. 67:537–544.

Gilpatrick, J.W. Jr., W.F. Perrin, S. Leatherwood, and L. Shiroma
1987 Summary of distribution records of the spinner dolphin, *Stenella longirostris*, and the pantropical spotted dolphin, *S. attenuata*, from the western Pacific Ocean, Indian Ocean and Red Sea. NOAA Tech. Memo. NOAA-TM-NMFS-SWFC-89, NMFS Southwest Fish. Sci. Cent., La Jolla, CA 92038, 42 p.

Hall, M.A., and S.D. Boyer
1990 Incidental mortality of dolphins in the tuna purse-seine fishery in the eastern Pacific Ocean during 1988. Rep. Int. Whaling Comm. 40:461–462.

Holt, R.S., and A. Jackson
1987 Report of a marine mammal survey of the eastern tropical Pacific aboard the research vessel *McArthur* July 29–December 6, 1986. NOAA Tech. Memo. NOAA-TM-NMFS-SWFC-77, NMFS Southwest Fish. Sci. Cent., La Jolla, CA 92038, 161 p.
1988 Report of a marine mammal survey of the eastern tropical Pacific aboard the research vessel *McArthur*, July 30–December 10, 1987. NOAA Tech. Memo. NOAA-TM-NMFS-SWFC-116, NMFS Southwest Fish. Sci. Cent., La Jolla, CA 92038, 143 p.

Mayr, E.
1970 Population, species and evolution. Harvard Univ. Press, Cambridge, 453 p.

Perrin, W.F.
1972 Color patterns of spinner porpoises (*Stenella* cf. *S. longirostris*) of the eastern Pacific and Hawaii, with comments on delphinid pigmentation. Fish. Bull., U.S. 70:983–1003.
1975 Variation of spotted and spinner porpoise (genus *Stenella*) in the eastern Pacific and Hawaii. Bull. Scripps Inst. Oceanogr. 21, 206 p.
1990 Subspecies of *Stenella longirostris* (Mammalia: Cetacea: Delphinidae). Proc. Biol. Soc. Wash. 103:453–463.

Perrin, W.F., and J.R. Henderson
1984 Growth and reproductive rates in two populations of spinner dolphins, *Stenella longirostris*, with different histories of exploitation. Rep. Int. Whaling Comm. Spec. Issue 6:417–430.

Perrin, W.F., J.M. Coe, and J.R. Zweifel
1976 Growth and reproduction of the spotted porpoise, *Stenella attenuata*, in the offshore eastern tropical Pacific. Fish. Bull., U.S. 74:229–269.

Perrin, W.F., D.B. Holts, and R.B. Miller
1977 Growth and reproduction of the eastern spinner dolphin, a geographical form of *Stenella longirostris* in the eastern tropical Pacific. Fish. Bull., U.S. 75:725–750.

Perrin, W.F., P.A. Sloan [Akin], and J.R. Henderson
1979a Taxonomic status of the "southwestern stocks" of spinner dolphin *Stenella longirostri* and spotted dolphin *S. attenuata*. Rep. Int. Whaling Comm. 29:175–184.

Perrin, W.F., W.E. Evans, and D.B. Holts
1979b Movements of pelagic dolphins (*Stenella* spp.) in the eastern tropical Pacific as indicated by results of tagging, with summary of tagging operations, 1969–76. NOAA Tech. Rep. NMFS SSRF-737, 14 p.

Perrin, W.F., E.D. Mitchell, J.G. Mead, D.K. Caldwell, and P.J.H. van Bree
1981 *Stenella clymene*, a rediscovered tropical dolphin of the Atlantic. J. Mammal. 62:583–598.

Perrin, W.F., M.D. Scott, G.J. Walker, F.M. Ralston, and D.W.K. Au
1983 Distribution of four dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern tropical Pacific, with an annotated catalog of data sources. NOAA Tech. Memo. NOAA-TM-NMFS-SWFC-38, NMFS Southwest Fish. Sci. Cent., La Jolla, CA 92038, 65 p.

Perrin, W.F., M.D. Scott, G.J. Walker, and V.L. Cass
1985 Review of geographical stocks of tropical dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern Pacific. NOAA Tech. Rep. NMFS SSRF-28, 28 p.

Peterson, C.L., and W.H. Bayliff
1985 Organization, functions, and achievements of the Inter-American Tropical Tuna Commission. Inter-Am. Trop Tuna Comm. Spec. Rep. 5, 56 p.

Punsley, R.G.
1983 Estimation of the number of purse-seiner sets on tuna associated with dolphins in the eastern Pacific Ocean during 1959–1980. Inter-Am. Trop. Tuna Comm. Bull. 18(3), 299 p.

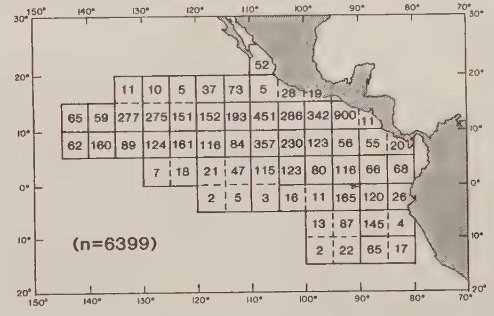
Reilly, S.B.
1990 Seasonal changes in distribution and habitat differences among dolphins in the eastern tropical Pacific. Mar. Ecol. Prog. Ser. 66:1–11.

Schnell, G.D., M.E. Douglas, and D.J. Hough
1982 Geographic variation in morphology of spotted and spinner dolphins (*Stenella attenuata* and *S. longirostris*) from the eastern tropical Pacific. Admin. Rep. LJ-82-15C, NMFS Southwest Fish. Sci. Cent., La Jolla, CA 92038, 213 p.
1985 Further studies of morphological differentiation in spotted and spinner dolphins (*Stenella attenuata* and *S. longirostris*) from the eastern tropical Pacific. Admin. Rep. LJ-85-04C, NMFS Southwest Fish. Sci. Cent., La Jolla, CA 92038, 30 p.

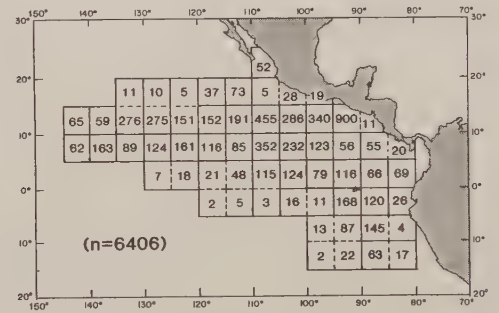
Young, T.L., and M.L. Van Woert
1987 PLOT88 software library. Plotworks, Inc., La Jolla, CA.

Appendix

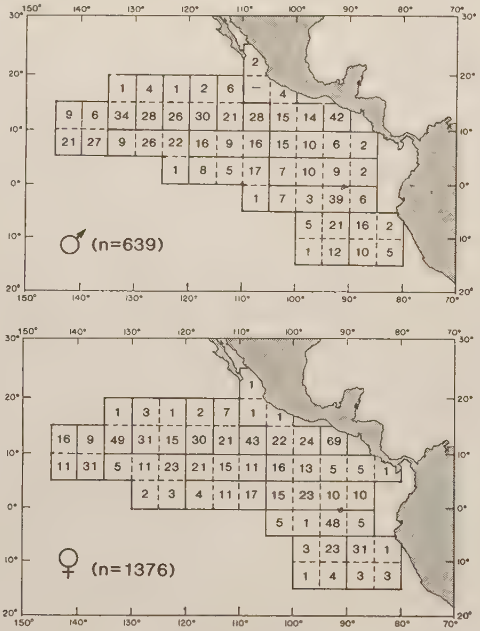
Sample sizes by 5-degree block and pooling for analyses of geographical variation in external morphology of the spinner dolphin (blocks separated by dashed lines were pooled).


150° 140° 130° 120° 110° 100° 90° 80° 70°
30° 20° 10° 0° 10° 20°
52
11 10 5 37 73 5 28 19
65 59 277 275 151 152 193 451 286 342 900 11
62 160 89 124 161 116 84 357 230 123 56 55 20
7 18 21 47 115 123 80 116 66 68
2 5 3 16 11 165 120 26
13 87 145 4
2 22 65 17
(n=6399)

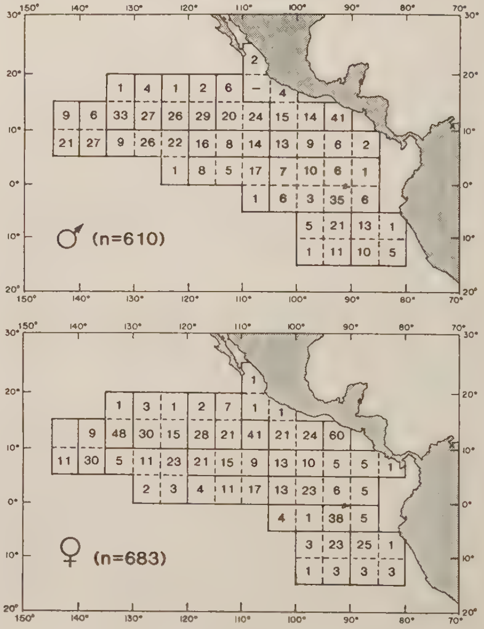
Appendix Figure 1
Ventral field (see Figure 13).


150° 140° 130° 120° 110° 100° 90° 80° 70°
30° 20° 10° 0° 10° 20°
52
11 10 5 37 73 5 28 19
65 59 276 275 151 152 191 455 286 340 900 11
62 163 89 124 161 116 85 352 232 123 56 55 20
7 18 21 48 115 124 79 116 66 69
2 5 3 16 11 168 120 26
13 87 145 4
2 22 63 17
(n=6406)

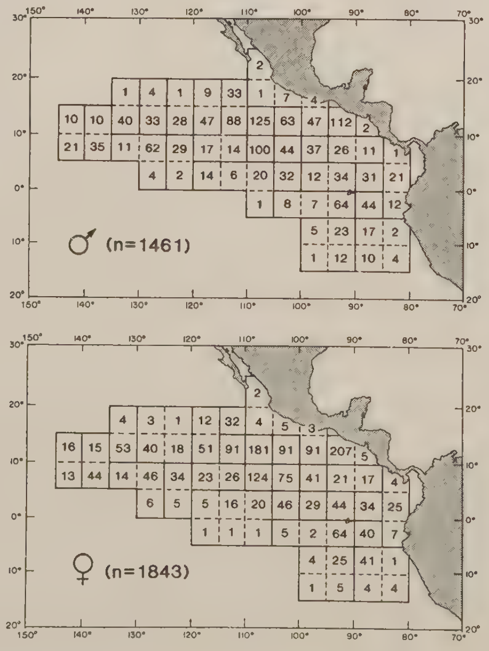
Appendix Figure 2
Cape (see Figure 15).


♂ (n=639)
♀ (n=1376)
150° 140° 130° 120° 110° 100° 90° 80° 70°
30° 20° 10° 0° 10° 20°

Appendix Figure 3
Dorsal fin (see Figures 15 and 17).


♂ (n=610)
♀ (n=683)
150° 140° 130° 120° 110° 100° 90° 80° 70°
30° 20° 10° 0° 10° 20°

Appendix Figure 4
Combined scores for ventral field, cape and dorsal fin (see Figures 18 and 19).


♂ (n=1461)
♀ (n=1843)
150° 140° 130° 120° 110° 100° 90° 80° 70°
30° 20° 10° 0° 10° 20°

Appendix Figure 5
Body length (see Figures 21 and 22).

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ASSESSEMENT OF BIOLOGICAL IMPACTS OF ARTIFICIAL REEFS AND FADS

BY

JEFFREY J. POLOVINA[1]

INTRODUCTION

A large volume of literature deals with the ecology at artificial reef sites--specifically with community composition, succession, biomass, and fishing success--whereas few studies address the broader biological impacts of artificial reefs and fish aggregating devices (FADs) on fish populations (Bohnsack and Sutherland 1985; Bohnsack 1989). The limited number of studies is certainly not due to a lack of interest but rather to the difficulty in collecting the appropriate date . To determine the possible biological impacts of artificial habitat in the presence of variations in the environment, fishing strategies, and gear, data must be collected from large-scale applications of artificial habitat on an appropriate spatiotemporal scale. The scale of most research or pilot applications of artificial habitat is too small to detect biological impacts on stocks even at a local level. Thus, much of the current thinking on the biological impacts of artificial habitat is speculative.

Often discussions on the impacts of artificial reefs and FADs distinguish between impacts due to aggregation and those due to "new production" (Bohnsack 1989). However, from both a management and biological perspective, it is important to make the distinction between aggregation that simply redistributes exploitable biomass and aggregation that attracts biomass not previously exploited and increases the exploitable biomass. Thus, it can be useful to consider the three types of impacts on the exploitable biomass and total stock due to the artificial habitat. First, FADs and artificial reefs can simply redistribute the exploitable biomass without increasing it or total stock size. Second, FADs and artificial reefs can aggregate previously unexploited biomass and increase the exploitable biomass but not the total stock size. Third, when stocks are limited by high relief habitat, artificial reefs can increase it and hence total stock size. Thus, these three types of impacts distinguish not only between the two types of aggregation but also total stock size and exploitable biomass. Because some of their biological aspects will differ, the three impacts will be discussed separately in subsequent sections; however, all three may occur to varying degrees in any artificial habital application.

IMPACTS DUE TO A REDISTRIBUTION OF EXPLOITABLE BIOMASS

For some resources, artificial habitat may primarily change the distribution of the exploitable biomass without increasing it or the total stock. For example, some of the resources exploited on the natural habitat move to the artificial habitat, or a highly mobile resource that moves between natural habitat may add artificial habitat to its route. This type of impact appears to be illustrated by flatfishes (Pleuronectidae) in a study by Polovina and Sakai (1989). They considered the impact of 50,000 ^{3} of artificial reefs deployed in Shimamaki Bay off Hokkaido, Japan, and found that, although flatfishes were caught in substantial numbers at the artificial reefs, no increase in flatfish landings could be attributed to the artificial reefs when landings from the entire bay were considered. In sonic tagging studies, flatfishes readily moved from natural habitat to artificial reefs but were not long-term residents at either sites (Kakimoto 1984). It was concluded that the artificial reefs redistributed the flatfishes but did not change their exploitable biomass (Polovina and Sakai 1989).

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In another instance, an application of artificial reefs in the Gulf of Thailand did not appear to increase the exloitable biomass for one resource but did change its allocation among user groups (Sinanuwong 1988). Concrete cylinder artificial reefs were deployed over a 1 × 4 nmi area about 2 nmi offshore on fishing grounds for threadfin *(Eleuteronemus tetraductylum)*. The area was closed to trawlers and push-netters, and the resource was allocated to small-vessel, village fishermen using gill nets (Sinanuwong 1988). Earlier village fishermen had fished this resource (for about 15 days in November-December) until the schools were depleted by trawlers and push-netters; however, after the deployment of the artificial reefs, they were able to fish the schools for at least a 6–month interval. The threadfin catch by the village fishermen was 1,746 kg (mean catch rate, 4.7 kg/trip) prior to the deployment of artificial reefs and increased to 5,562 kg (mean catch rate, 8.3 kg/trip) after deployment (Sinanuwong 1988).

The Shimamaki study (Polovina and Sakai 1989) could not identify any biological impacts from the redistribution of exploitable biomass, but there were potential impacts: Because the density of the exploitable biomass per area of habitat had been reduced, growth and also natural mortality of the stock may have been affected. If the ecosystems at the natural and artificial habitats differed, some prey and predators may have been impacted as well. However, the greatest impact may be a reduction in exploitable biomass if fishing at the artificial habitat is not restricted. The siting of artificial habitat usually allows them to be more accessible to fishermen year-around and often to support a higher density of fishes than natural habitat. The higher density may increase the catchability of the fishing gear, whereas the greater accessibility increases fishing effort and can result in higher fishing mortality. An increase in fishing mortality will decrease the exploitable biomass in the area exploited. Whether the decrease in exploitable biomass results in lower future catches or recruitment to the fishery either locally or in an adjacent region depends on the stock dynamics. If the stock is migratory, then heavy fishing mortality in one region will result in lower levels of exploitable biomass in adjacent regions. If there is a strong regional stock-recruitment relationship, then heavy local fishing mortality could reduce future recruitment.

The Thailand example (Sinanuwong 1988) illustrates an application of artificial habitat that likely resulted in a reduction in fishing mortality, because the increase in catches by the village fishermen was probably less than the catches previously taken by the more efficient trawlers and push-netters. This example also shows that artificial habital can result in a change in the types of fishing gear used; such a change may impact the species caught, catchability, and fishing mortality. Further, since the species composition of the catches at the artificial habitat may differ from that at the natural habitat, fishing mortality may increase for some species but decrease for others as effort shifts from natural to artificial habitat.

IMPACTS DUE TO INCREASED EXPLOITABLE BIOMASS BUT NOT TOTAL STOCK SIZE

Aggregation may not only cause a resource to be redistributed but also increase the resource exploited by the fishery. Artificial habitat might aggregate juveniles. Aggregation makes them more accessible to capture and hence increases the exploitable biomass by lowering the size at entry to the fishery. Conversely, aggregation might make available to fishing gear a portion of the resource that had been distributed at a low density and not previously exploited. An extreme case of this would be a resource that had not been fished because it was distributed widely at a low density at a natural habitat. An artificial habitat will aggregate the resource at a density sufficient to support a fishery, and the resource can then be exploited. From a fisherman's perspective, if a resource is not overexploited, it does not matter whether exploitable biomass is increased by aggregating unexploited biomass to artificial habitat or from new production which increases stock size. In both cases, increased catches will be achieved without increased effort.

The impact of FADs on tuna in the Philippines appears to represent this type of aggregation. The use of FADs (payaos) together with purse seines or ring nets in the Philippines was introduced in the tuna fishery in early 1970's. As a result, tuna catches rose from less than 10,000 metric tons (t) in 1970 to 266,211 t in 1986, representing 20% of the national marine catch (Aprieto 1988). Over 90% of the tunas caught at the FADs are less than 1-year-old and at about one-half the length at first maturity (Aprieto 1988). Some concern exists that the heavy fishing mortality with the small length at entry may result in growth and recruitment overfishing (Aprieto 1988). The question of whether FADs could cause growth overfishing has been examined by Floyd and Pauly (1984). Four factors are necessary for growth overfishing: i) presence of small fish on the fishing ground, ii) use of gear capable of catching small fish, iii) a market for small fish, and iv) high exploitation rates. All four of these factors are present in the Philippine tuna fishery. Using an exploitation rate of 0.7-0.8 for skipjack tuna *(Katsuwonus pelamis)* and yellowfin tuna *(Thunnus albacares)* with the Beverton and Holt (1966) yield equation, the yield per recruit declines by an estimated 50% when the size at entry drops from one-half to one-fourth the asymptotic length (Floyd and Pauly 1984). The recent decline in landings from this fishery may be due in part to growth overfishing (Floyd and Pauly 1984). Further, there is some evidence that the natural mortality of juvenile tunas is greater at FADs than for schools in the open ocean, suggesting that FADs have increased natural mortality as well (Aprieto 1988).

The biological impacts of this type of aggregation include all the impacts associated with aggregation that just redistributes exploitable biomass. However, when aggregation increases the exploitable biomass, other impacts occur and depend on the dynamics between fish aggregated and those not aggregated. Clark and Mangel (1979) developed a model for tuna purse seining in which tunas move from subsurface populations to surface schools which are fished. Applying this model to the tuna fishery with FADs shows that the potential impact of FADs on the stock depends primarily on whether the rate of movement the unaggregated population to the FADs, as well as the mortality of the unaggregated population, exceeds the intrinsic rate of population increase (Samples and Sproul 1985). If the rate that tunas aggregate at FADs plus non-FAD mortality exceeds the population growth rate, then high fishing mortality at the FADs alone can drive the fishable population to zero. The relationship between catches at a FAD and effort follows the typical dome-shaped production curve. The biological impact in this case is that excessive fishing effort at FADs can result in recruitment overfishing. However, when the growth of the population exceeds the non-FAD mortality and the rate of aggregation to the FADs, no amount of fishing at the FADs can exhaust the total population (Samples and Sproul 1985). In this case, catch increases with effort to an asymptotic value. The biological impact in this case is that increasing fishing effort on aggregations cannot increase the fishing mortality beyond a certain level. While the Clark and Mangel (1979) model was applied specifically to the tuna fishery at FADs, the results also apply to demersal resources aggregated at artificial reefs.

IMPACTS WHEN TOTAL STOCK SIZE INCREASES

In theory, providing additional habitat could increase the population size for some habitat-limited stocks. For example, the habitat provided by artificial reefs might result in substrata for additional food, shelter from predation, settlement habitat, and lower densities at natural reefs (Bohnsack 1989). However, despite the large number of studies on artificial reefs, very little direct evidence indicates that artificial reefs can increase the population size of a stock (Bohnsack 1989).

Polovina and Sakai (1989), however, do provide some evidence that artificial reefs can increase the total stock. Fishery catches for octopus *(Octopus dofleini)* from two adjacent fishing grounds in a bay with a 27 km coastline near Shimamaki, Hokkaido, Japan, were examined before and after the deployment of about 50,000 m^3 of artificial reefs. They found that octopus were caught at the artificial reefs, and when the total fishing ground catches were considered, the increase in octopus landings was explained by the increase in the volume of artificial reefs. The data from two adjacent regions in the same bay made it possible to compare relative changes in catches and catch rates as a function of artificial reef volume in each bay. While changes in environment or fishery economics could alter catches and catch rates in each region, the relative catches and catch rates should be unaltered by these factors and reflect only the impact due to the artificial reefs. The magnitude of the increase in octopus catches attributed to the artificial reefs was about 90 t or about 1.8 kg/m^3 of artificial reef volume per year. It was concluded that the artificial reefs increased the exploitable biomass of octopus. This increase possibly came from either an aggregation of octopus from habitat not previously exploited or from new biomass due to the additional habitat. Unfortunately, no surverys of octopus abundance and size structure over the natural habitat and arificial reefs before and after the deployment were conducted to complement the fishery data and determine whether the reefs were aggregating the octopus or actually increasing the population size. However, this issue was addressed by examining the change in catches in the two adjacent regions. It was hypothesized that, if artificial reefs aggregated octopus from the entire bay, then as the octopus moved to the region with the large reef volume, an increase in octopus catches in the region with the large volume of artificial reefs would be accompanied by a corresponding decline in catches in the adjacent region with the low volume of artificial reefs. But if the artifical reefs increased the population of octopus, changes in catches in each region would be independent of the artificial reef volume in the adjacent region and depend only on the volume within each region. The catch and effort data indicated that the catches in each region were independent of the artificial reef volume in the adjacent regions, consistent with the hypothesis that the artificial reefs did indeed increase the population of octopus (Polovina and Sakai 1989).

When the exploitable biomass in a region is heavily fished, the density of the resource above the size at entry to the fishery is very low relative to the pre-exploitation density. Thus, habitat is not likely to limit the population above the size at entry to the fishery, and artificial reefs that provide more habitat for this portion of the population are not likely to increase new production. If artificial reefs are to increase new production of this resource, they might provide habitat to improve the following: Larval settlement, juvenile growth, and a reduction in juvenile natural mortality. Thus, biological impacts of artificial reefs that increase total stock size are likely to include one or more of the following: an increase in postlarval settlement, juvenile growth, or juvenile survival. However, just as with the impacts from aggregation, an increase in fishing effort and hence fishing mortality may also occur as the fishery responds to more accessible habitat and higher catches.

In the absence of studies that quantify an increase in stock size due to artificial reefs, two simple approaches--one based on yield from natural habitat and the other based on the standing stock estimates at artificial reefs, together with an estimate of yield to biomass--can provide useful estimates of the maximum potential enhancement due to artificial reefs. For the first approach, yield per area of artificial reefs is simply estimated from fishery yields per area of corresponding natural habitat: the resulting figure is adjusted upwards for the observed higher catches between artificial reefs and natural habitat. For example, to estimate, potential fishery catches from artificial reefs in the tropics, the range of fishery production from coral reefs must first be considered. Annual fishery production per area of coral reef habitat ranges from less than 1 t/km^2 to 18 t/km^2, with values clustering around 5 t/km^2 (Marten and Polovina 1982). Biomass on artificial reefs is generally seven times greater than on natural habitat (Stone et al. 1979). If artificial reefs can support 10 times the exploitable biomass of natural coral reefs, then an average annual value for the fishery catches from an artificial reef in the tropics is 50 t/km^2 or 10 times higher than those from a coral reef. This is equivalent to a yield of 0.05 kg/m^3. If as an upper bound this yield is assumed to come from only 1 m of vertical relief, then the yield per reef volume is 0.05 kg/m^3.

The second approach to estimating the new production of an artificial habitat uses the biomass estimated from local artificial reefs and then estimates the potential fishery yield as a fraction of that biomass. The Beverton and Holt (1966) yield equation can be used to determine the fraction of the biomass at the reef that can be harvested on a sustainable basis, if estimates of a number of population parameters are available (Beddington and Cooke 1983). However, in the absence of estimates of population parameters, an upper bound for sustainable catch can be taken as $0.5^* \; M^* B_O$, where M is the natural mortality and B_O is the unexploited exploitable biomass (Beddington and Cooke 1983). For example, the range of biomass estimates observed on tropical and subtropical artificial reefs is 26–698

g/m^2 (Stone et al. 1979). More recently, a value of 1,266 g/m^2 was documented (Brock and Norris 1989). Taking an average value for this range of 650 g/m^2 as an average estimate of the unexploited exploitable biomass, the fishery catches can be estimated by multiplying this value by an estimate of 0.5* M. For a tropical, fast-growing and short-lived species. M equaling 0.7 might be appropriate. Then a biomass of 650 g/m^2 at the artificial reef would support a miximum annual fishery production of about 35% of the unexploited exploitable biomass or 228 g/m^2. Again, if yield per square meter is assumed to be due to just 1 m of vertical relief, then an upper bound for the potential fishery yield from an artificial reef in this example is 0.2 kg/m^3.

Studies have documented total catches at artificial reefs of 8 kg/m^3 of artificial reef volume from the Philippines and 5–20 kg/m^3 from Japan (Sato 1985: Bojos and Vande Vusse 1988). Of course, these catches include fishes aggregrated by the reefs as well as any new production due to the reefs. Based on the examples previously considered, estimates of new production due to artivicial reefs is on the order 0.02–0.5 kg/m^3, indicating that these levels of catches from the artificial reefs are primarily from fishes aggregated by the reefs and greatly exceed the maximum catches that could be expected from new production.

CONCLUSIONS

1. Artificial habitat may function in three ways: it may redistriute exploitable biomass, increase exploitable biomass by aggregating previously unexploited biomass, or improve aspects of survival and growth and provide new production. In all three functions, artificial habitat has the potential to alter fishing effort, gear, size at entry to the fishery, species targeted, and hence fishing mortality. The impact of a change in fishing mortality on the stock depends on the relative level of exploitation and the rate of movement of the resource to the artificial habitat.

2. In artificial reef applications, it is possible to estimate the maximum catches from new exploitable biomass due to the artificial reef and compare this with the actual catches to determine the extent to which the artificial reef is serving as a benthic aggregating device. The data examined in this paper indicate that the potential new production due to artificial reefs is low relative to the catches at artificial reefs; hence, the primary role of artificial habitat is to aggregate resources.

3. More rigorous experimental designs are needed to document the biological impacts of artificial habitat. These designs need to use large numbers of artificial habitat to ensure sufficient statistical power exists to detect impacts in the presence of considerable natural variation which occurs in many marine systems. Also, they may need to have a control site without artificial habitat. A time series of data both before and after the deployment of the artificial habitat should be collected at the treatment and control sites. Fishery-dependent and fishery-independent data should be collected on an appropriate spatial scale and resolution to detect impacts at the artificial and natural habitats.

4. Since artificial habitat changes the spatial distribution and density of resources and the fishing effort, standard fishery models which do not treat this spatial dimension may not represent adequate models. Application of the Clark and Mangel (1979) model has proved useful for FADs. Further application of this model and habitat and diffusion models should result in more realistic models to evaluate potential impacts of artificial habitat (Mullen 1989; MacCall in preparation).

REFERENCES

APRIETO, V.L., 1988. Aspects of management of artificial habitats for fisheries: The Philippine situation, p. 102–110. **In** Report of the workshop on artificial reefs development and management, Penang, Malaysia. ASEAN/SF/88/GEN/8

BEDDINGTON, J.R. AND J.G. COOKE, 1983. The potential yield o fish stocks. **FAO Fish. Tech. Pap.,** (242): 47 p.

BEVERTON, R.J.H. AND S.J. HOLT, 1966. Manual of methods for fish stock assessment Part II – Tables of yield functions. **FAO Fish. Tech. Pap.,** (38): 67 p.

BOHNSACK, J.A., 1989. Are high densities of fishes at artificial reefs the result of habitat limitation or behavioral preference? **Bull. Mar. Sci.** (44): 631–645.

BOHNSACK, J.A. AND D.L. SUTHERLAND, 1985. Artificial reef research with recommendations for future priorities. **Bull. Mar. Sci.** (37): 11–39.

BOJOS, R.M. AND F.J. VANDE VUSSE, 1988. Artificial reefs in Philippine artisanal fishery rehabilitation, p. 162–169 **In** Report of the workshop on artificial reefs development and management, Penang, Malaysia. ASEAN/SF/88/GEN/8

BROCK, R.E. AND J.E. NORRIS, 1989. An analysis of the efficacy of four artificial reef designs in tropical waters. **Bull. Mar. Sci.** (44): 934–941.

CLARK, C.W. AND M. MANGEL, 1979. Aggregation and fishery dynamics: A theoretical study of schooling and the purse seine tuna fisheries. **Fish. Bull., U.S.** (77): 317–337 Floyed. J.M. and D. Pauly. 1984. Smaller size tuna around the Philippines–can fish aggregating devices be blamed? **FAO INFOFISH Marketing Digest** (5): 25–27.

KAKIMOTO, H., 1984. Ecological study of the Bastard halibut or hirame *(Paralichthys olivaceus)* in the sea referring to the moving of adult fish, p. 183–189. In Fisheries in Japan Flatfish. Japan Marine Products Photo Materials Association. Tokyo.

MACCALL, A.D., in preparation. Geographical population dynamics, harvesting and environmental management. Southwest Fisheries Center, 3150 Paradise Drive, Tiburon, CA 93942.

MARTEN G.G. AND J.J. POLOVINA, 1982. A comparative study of fish yields from various tropical ecosystmes, p. 255–289 **In** Pauly, D. and G.I. Murphy (eds.) Theory and management of tropical fisheries. ICLARM Conference Proceedings 9, 360 p. International Center for Living Aquatic Resources Management, Manila, Philippines and Division of Fisheries Research, Commonwealth Scientific and Industrial Research Organisation, Cronulla, Australia.

MULLEN A.J., 1989. Aggregation of fish through variable diffusivity. **Fish. Bull.,U.S.** (87): 353–362 Polovina, J.J. and I. Sakai, 1989. Impacts of artificial reefs on fishery production in Shimamaki, Japan. **Bull. Mar. Sci.** (44): 997–1003.

SAMPLES, K.C. AND J.T. SPROUL, 1985. Fish aggregating devices and open-access commercial fisheries: A theoretical inquiry. **Bull. Mar. Sci.** (37): 305–317.

SATO, O., 1985. Scientific rationals for fishing reef design. **Bull. Mar. Sci.** (37): 329–335.

SINANUWONG, K., 1988. Artificial reefs construction in Nakornsrithammarat Province, p. 130–134 In Report of the workshop on artificial reefs development and management, Penang, Malaysia. ASEAN/SF/88/GEN/8

STONE, R.B., H.L. PRATT, R.O. PARKER, JR. AND G.E. DAVIS. 1979. A comparison of fish populations on an artificial and natural reef in the Florida Keys. **Mar. Fish. Rev.** (41): 1–11.

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A GLOBAL PERSPECTIVE ON ARTIFICIAL REEFS AND FISH AGGREGATING DEVICES

BY

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PREFACE

In recent years, research on artificial reefs and fish aggregating devices (FADs) and their application to fishery enhancement has increased. For example, the Third International Conference on Artificial Reefs in 1983 had 43 presentations and 14 posters that covered work from 7 countries. At the Fourth Conference held in 1987, 350 participants from 26 nations attended and made 94 oral and 37 poster presentations on research and applications from 19 countries (Seaman et al. 1989).

Centers of activity for artificial habitats include Australia, Japan, Southeast Asia, the Caribbean, the Mediterranean, Pacific islands, and North America. This paper reviews four applications and worldwide impacts of artificial reefs and FADs. The applications are 1) enhancement of artisanal fishing, 2) small-scale commercial fishing, 3) recreational fishing and diving, and 4) mitigation of habitat loss due to shoreside development.

ARTISANAL FISHERIES

Artisanal fishermen have developed many artificial reefs and fish aggregating device (FAD) designs to create fishing grounds close to their villages. The structures have traditionally been constructed with sticks, poles, bamboo, or bundles of brush, but more frequently are being made from concrete and scrap tires.

In the Philippines, a widely used artificial reef module is made from bamboo poles that are arranged in a tripod, weighted with stones, and covered with coconut palm fronds. The units are usually placed in calm, shallow coastal waters; however, when these reefs are used in deeper water, a FAD may be attached to mark their location and to attract pelagic fishes. Large-scale deployments of reefs and FADs are used as part of regional development programs. Approximately 16,000 pyramid bamboo modules in clusters of 50 have been set along 40 km of coastline in the central Visayan Islands and over 8,000 bamboo modules have been deployed in the Samar Sea-Ticao Pass Project (Miclat 1988). These artificial reefs are planned, constructed, deployed, and maintained by the village fishermen (Miclat 1988). The reefs are conveniently located, and the value of the catches during the first year of deployment can exceed the installed cost of the reefs (Miclat 1988). For example, the bamboo pyramids used in the Central Visayan Project had an estimated installed cost of US\$4.00/m^3 while annual harvests are 8kg/m^3; therefore, if all the fish caught were sold, the installed cost of the reef would be repaid in 9 months (Bojos and Vande Vusse 1988). Recently, artificial reefs made from concrete reinforced with bamboo have been used instead of bamboo because the bamboo reefs only have a 4-year lifespan (Bojos and Vande Vusse 1988).

While FADs are used by artisanal fishermen in many countries, the situation in the Philippines is unique because artisanal fishermen fish FADs are deployed by commercial purse seiners. About 3,000

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FADs (payaos) are used for tuna fishing in the Philippines (Aprieto 1988). Although owned and deployed by purse seiners, the FADs are also proving very beneficial to the artisanal fishermen who are allowed to handline around the FADs for large tunas swimming at depths too deep to be caught in purse seine nets (Aprieto 1988).

In Cuba and Mexico, artisanal fishermen use artificial reefs to attract lobsters *(Panulirus argus)* and facilitate their capture. In Cuba, mangrove branches are used to form shelters, which consists of flat layers of branches, about 2 m in length and width, raised about 10–15 cm above the ocean bottom by cross branches. These shelters are set in depths of 4–6 m. Fishermen catch the lobsters by shaking the shelters and netting the lobsters as they leave. In the Gulf of Batabano, Cuba, cooperatives use 120,000 lobster shelters and harvest 7,000 tons (t) of lobsters from them (National Research Council 1988). In Mexico, similar shelters have been used since the late 1960's, but many are now made from ferroconcrete and corrugated roofing material.

Thailand's Department of Fisheries has used old tires and concrete cubes to construct artificial reefs for artisanal fishermen in the Gulf of Thailand. These reefs, placed on soft-bottom areas, provide hard substrata and vertical relief, which attract valuable snappers and groupers normally not found at soft-bottom sites. In one application, the reefs were seeded with green mussels (National Research Council 1988). In another case, artificial reefs were placed on fishing grounds in the Gulf of Thailand for threadfin *(Eleuteronemus tetradactylum)*. The area was closed to trawlers, thus allocating the resource to village fishermen using gill nets from small vessels (Sinanuwong 1988). Before deployment of the artificial reefs, village fishermen fished this resource for about 15 days in November-December, before the schools were depleted by trawlers and push-netters. However, after the deployment of the artificial reefs, trawlers and push-netters were unable to operate in the area, and village fishermen were able to fish the schools for at least 6 months. Prior to deployment of the artificial reefs, threadfin catch by village fishermen was 1,746 kg, with an average catch rate of 4.7kg/trip, but after the deployment of the artificial reefs, threadfin catch by the same fishermen increased to 5,562 kg, with an average catch rate of 8.3 kg/trip (Sinanuwong 1988). The Thailand Goverment is considering plans to expand its artificial reef program by using concrete cube modules (volumes of 1–and 2m^3) to construct large artificial reefs with volumes of 25,000–50,000 m^3 and covering areas of 50–100 km^2 (Sungthong 1988). These large reefs would close large areas to trawling and create fishing sites for artisanal fishermen (Sungthong 1988).

The Malaysian Department of Fisheries has an artificial reef program, which, by 1988, deployed 65 artificial reefs made from over 505,000 scrap tires, 7 reefs made from sunken ships, and 4 reefs made from pyramids of concrete pipes (Hung 1988). The tire reefs consist of modules of tires tied into pyramids with polyethylene rope. The number of tires per artificial reef site varied: almost 40% of the reefs had less than 1,000 tires but 5% were composed of more than 30,000 tire (Hung 1988). The objective of the Malaysian artificial reef program is to enhance biological productivity and fishery resources in coastal waters. To prevent the overfishing of resources aggregated at the artificial reefs, the Department of Fisheries prohibits fishing within 0.5 mile of the artificial reefs (Hung 1988). The Malaysian artificial reef program is expanding, and by 1990, the artificial reefs are expected to contain a total of 2 million tires (Hung 1988).

In summary, artificial reefs and FADs can reduce travel and search time for artisanal fishermen and improve the catchability of their gear. As long as the total fishing effort on the resource is not sufficient to result in overfishing, the effects of these structures on the resource are not harmful. Competition between gears and fishermen at the artificial reefs and FADs is a potential problem if effort is not regulated, but these structures could also serve to redistribute fishing effort to resolve competition. Artificial reefs may be useful in closing areas to trawling to protect juveniles in shallow nursery grounds and to provide fishing sites for artisanal fishermen using gear that captures older fish. The application of artificial reefs and FADs should be a community project: fishermen should be involved in their planning construction, and maintenance. Artificial reefs have potential to serve as habitat for extensive mariculture. Artificial reefs and FADs built with local materials have appeal, but care should be taken to avoid depleting local forests and mangroves. Longer lasting reefs built from scrap tires and concrete may ultimately prove more economical.

SMALL-VESSEL COMMERCIAL FISHERIES

Small-vessel commercial fishermen typically sell all of their catch and use larger vessels with greater fishing power, hydraulics, depth finders, inboard engines, and so on. In many developed countries, these small-vessel commercial fishermen are operating at marginal economic levels, and governments see the use of artificial reefs and FADs as possibly being beneficial to the operations of these fishermen.

The Japanese have the most extensive system of artificial reefs to assist the small-vessel commercial fishermen. Since 1976, the Japanese have spent over US$l billion to construct and deploy artificial reefs with an enclosed volume exceeding 17 million m^3 (Grove et al. 1989). As a result, 9.3% of the total nearshore habitat down to 200 m has been covered with artificial reefs (Yamane 1989). The artificial reefs reportedly are popular with fishermen, because they increase catches and decrease operating costs (Yamane 1989). Whether the artificial reefs actually increase fishery catches has been addressed in an analysis of fishery catches bofore and after the deployment of 50,000 m^3 of artificial reefs in a small bay in Hokkaido. Japan (Polovina and Sakai 1989). This study found that, while several resources were caught at the artificial reefs, an increase in landings for only one resource, octopus *(Octopus dofleini)*, was attributed to the artificial reefs (Polovina and Sakai 1989). It was estimated that the artificial reefs increased the octopus catches by 1.8 kg/m^3 of artificial reef. A survey of fishermen from this bay found that 53% used the artificial reefs regularly, 12% used them only when fishing elsewhere was poor, and 36% did not use them at all (Polovina and Sakai 1989). Further, 33% of the fishermen thought the reefs had expanded the amount of productive habitat, 38% thought the reefs did not increase the productive habitat, and 30% were unable to decide (Polovina and Sakai 1989).

In the Mediterranean Sea, Italy, France, and Spain have modest artificial reef and FAD projects. The coastal environment in many parts of the Mediterranean Sea has a soft bottom, water with a high nutrient level that is not fully recycled by the ecosystem, and many nearshore fisheries that are overfished, in part, because of illegal trawling. The objectives of these programs include 1) protection of nursery grounds from illegal trawling, 2) attraction of pelagic and benthic species that use hard substrata, and 3) provision of substrata for shellfish farming and nutrient recycling in eutrophic environments. Initially a variety of materials, including car bodies and ships, was used as artificial reefs, but most recent and planned artificial reefs consist of concrete cubes or blocks. A study of a 4,300 m^3 concrete block artificial reef in Italy found that the reef increased both mussel and fish catches (Bombace 1989). The net proceeds for a fisherman operating within the reef were 2.5 times greater than those operating outside the reef (Bombace 1989). In the eutrophic waters such as those of the Adriatic, the cost of the reefs is recovered about three times in 7 year (Bombace 1989). Initially, trawlers were opposed to the reefs since the area was closed to trawling, but they changed their attitude as they experienced good catches of large fish along the edges of the reef zone (Bombace 1989). Typically in Italy, when artificial reefs are deployed, the area covered by reefs is designated as a marine zone, and activities and users in the zone are regulated. Problems have been encountered in administering the usage of these zones, often because the marine resources in the zones are not sufficient for the demand (Bombace 1989). Commercial fishermen in Italy are promoting the development of more marine zones protected by artificial reefs, France has less interest in developing new zones, and Spain is just beginning to evaluate artifical reefs (Bombace 1989).

Other nations have deployed artificial reefs and FADs to assist commercial fishermen. For example, 19 areas around Taiwan have artificial reefs built from concrete blocks deployed in 20–40 m depths on flat, sand or pebble bottoms to improve fishing sites (Chang 1985).

In Jamaica, artificial reefs made from scrap tires weighted with rocks or concrete are used to create fishing grounds near fishing villages and to provide habitat in areas closed to fishing (Haughton and Aiken 1989). Most South Pacific island use FADs widely to enhance catches of offshore pelagic fishes. An evaluation of FADs in American Samoa showed that their use could significantly increase catch per unit effort (CPUE) of offshore pelagic fishes for a troll fishery (Buckley et al. 1989). However, replacing lost FADs is a permanent job for fishery departments since the lifespan of FADs anchored in unprotected ocean around Pacific islands is often only a few years. Further, FADs do not always increase catches significantly; a study in Puerto Rico found only a slight increase in catches with FADs (Feigenbaum et al. 1989).

Increased CPUE due to artificial reefs and FADs alone may not be justification for their use by commercial fishermen when they receive heavy and unregulated usage. Since artificial reefs and FADs are usually located in accessible sites, they produce an increase in fishing effort and possibly an increase in the catchability of the gear and, hence, an increase in fishing mortality. Concern has been expressed that increased fishing mortality may occur even with FADs (Floyd and Pauly 1984). However, even if artificial reefs and FADs do not have a detrimental impact on the exploited stocks, they still may not be beneficial economically. An economic study of commercial open-access fisheries around FADs in Hawaii found that, even if high levels of fishing at FADs do not result in recruitment overfishing and if fishing effort is unregulated, installation of FAD networks will not generally increase fishermen's aggregate profit (Samples and Sproul 1985). Further, deployment of FADs could result in decreases in employment, harvest levels, and sustained gross revenues. The limiting of commercial fishing effort at FADs is seen as a means of preventing these detrimental impacts (Samples and Sproul 1985).

RECREATIONAL FISHING AND DIVING

Artificial reefs and FADs are popular with recreational fishermen and divers because they provide convenient sites with concentrations of fishes; such usage is widespread throughout the United States. Reefs and FADs are constructed and deployed by sport fishing and diving organizations and State fishery departments. The most common materials used are ships, concrete, tires, and stone rubble. In the Gulf of Mexico, 4,000 oil and gas rigs function as artificial reefs (Mogurrin et al. 1989). Oil companies are required to remove these oil and gas structures once they are no longer producing. One use for them is to move them into shallower water to increase their effectiveness as artificial reefs. However, given the large open construction of these structures, there is some question as to the effectiveness of these structures as artificial reefs.

Local government agencies support artificial reefs for recreational fishing and diving in the United States and Australia. In the United States, over one-half of the State fishery agencies have artificial reef programs and spent an average of US$1.5 million annually on the construction and deployment of artificial reefs and FADs (McGurrin et al. 1989). A survey of fisherman and sport divers in southern Florida found that about 28% of the recreational fishermen and 14% of the sport divers regularly used artificial reef sites (Milon 1989). In Australia, artificial reefs from tires assembled in a tetrachedron create fishing and diving sites for recreational fishermen and divers. A total of 34,000 tires was used at one site in Western Australia, and the A$205,000 cost of the program was justified on the basis that the artificial reef would increase revenues in the local community through an increase in activity and hence consumer spending in sport fishing and diving (Young 1988).

The reefs and FADs concentrate both fish and fishermen and, as a result, some concerns over the resource and the conflicts between users have been raised (Samples 1989). Two forms of conflicts at artificial reefs and FADs have been observed: competition over a common stock, and conflicts from user congestion (Samples 1989). An example of the former occurs between commercial pole-and-line boats and recreational trollers around FADs in Hawaii. A pole-and-line vessel can capture all of the skipjack tuna *(Katsuwonus pelamis)* around a FAD, leaving nothing for recreational trollers in the short term. On the other hand, conflicts due to user congestion occur when many users are concentrated around a reef or FAD, often with various types of gear, such as purse seiners and trollers or handlining and diving gear. Various approaches that restrict access, limit effort, or segregate users in space and time may resolve these conflicts (Samples 1989). Of course, carefully planned artificial reefs and FADs also can serve to shift effort away from heavily used natural sites.

Artificial reefs for recreational uses are often constructed and deployed by fishing and diving clubs without the resources or inclination to properly research the siting, design, and materials. Experience in Florida and other states, where a large number of artificial reefs of various materials have been deployed by numerous user groups, indicates that if attention is not given to proper siting and materials, the artificial reefs may be ineffective and even damaging (Andree 1988). It has been recommended that a Florida artificial reef plan be developed to establish standards for siting, design, and materials and to establish a central artificial reef permitting maintenance system and a monitoring system (Andree 1988).

MITIGATION FOR HABITAT LOSS AND HABITAT ENHANCEMENT FOR RESERVES

Applications of artificial reefs for uses other than to specifically increase fishing success include providing habitat to mitigate the loss of habitat due to coastal development or pollution and to improve habitat in marine reserves. The loss of rocky habitat due to nearshore filling was successfully mitigated with a 2.83 ha quarry rock artificial reef in Puget Sound, Washington (Hueckel et al. 1989). On the Pacific coast of Costa Rica, 5,000 scrap tires were used to construct new habitat to protect marine fauna rather than for fishing (Campos and Gamboa 1989). The reef, used by juvenile and adult fishes, was not marked, apparently to prevent fishermen from finding it and fishing the area.

In the case of mitigation, it is important to be sure that the artificial reefs are an appropriate habitat, are properly sited to replace the lost habitat, and are not adversely impacting other species. For example, species that use flat, low habitat may be adversely impacted if artificial reefs are deployed. A study in Puget Sound, Washington, found that the composition of benthic organisms at potential artificial reef sites serves as a useful predictor of the fish species that will subsequently colonize the artificial reef (Hueckel and Buckley 1989). The use of artificial reefs just to increase habitat for reef-associated species is questionable when one considers that even large artificial reefs only represent a very small fraction of the available natural reef habitat in any area.

SUMMARY

Experience in many countries has shown that properly constructed and sited artificial reefs and FADs can create convenient fishing sites. These structures have proven particularly effective for artisanal applications in which fishing effort is relatively low. However, since these structures serve to change the distribution of fishing effort and fishes, they must be viewed within an overall fishery management plan. Their impacts need to be considered in a broad socioeconomic context, rather than just in terms of changes in CPUE. A number of countries are finding that, in the presence of heavy effort, artificial reefs and FADs alone may not be economically beneficial. Measures that regulate gear and effort at artificial reef and FAD sites may be required to avoid resource overfishing and user conflicts and to improve fishery economics.

While the literature is full of studies on the ecology at artificial structures, studies on the broader fishery management and socioeconomic impacts of these structures are lacking. For there to be progress in the applications of artificial reefs and FADs, scientists and managers must understand and apply these structures within an overall fishery management system.

REFERENCES

ANDREE, S. (ed.), Florida artificial reef summit. Florida Sea Grant College, Sea Grant Rep. 93, 70 pp.
1988

APRIETO, V.L., Aspects of management of artificial habitats for fisheries: The Phillippine situation. In: Report of the workshop on artificial reefs development and management and management, Penang, Malaysia. ASEAM/SF/88/GEN/8: 102–110.
1988

BOJOS, R.M. AND F.J. VANDE VUSSE, Artificial reefs in Philippine artisanal fishery rehabilitation. In: Report of the workshop on artificial reefs development and management, Penang, Malaysia. ASEAN/SF/88/GEN/8: 162–169.
1988

BOMBACE, G., Artificial reefs in the Mediterranean Sea. Bull. Mar. Sci. 44: 1023–1032.
1989

BUCKLEY, R.M.,D.G. ITANO AND T.W. BUCKLEY, Fish aggregation device (FAD) enhancement of offshore fisheries in American Samoa. Bull. Mar. Sci. 44: 942–949.
1989

CAMPOS, J.A. AND C. GAMBOA, An artificial tire-reef in a tropical marine system: A management tool. Bull. Mar. Sci. 44: 757–766.
1989

CHANG, K.H., Review of artificial reefs in Taiwan: Emphasizing site selection and effectiveness. Bull. Mar. Sci. 37: 143–150.
1985

FEIGENBAUM, D., A. FRIEDLANDER AND M. BUSHING. Determination of the feasibility of fish attracting devices for enhancing fisheries in Puerto Rico. Bull. Mar. Sci. 44: 950–959.
1989

FLOYD, J.M. AND D. PAULY, Smaller size tuna around the Phillippines – can fish aggregating devices be blamed? FAO INFOFISH Marketing Digest 5: 25–27.
1984

GROVE, R.S.; C.J. SONU AND M. NAKAMURA, Recent Japanese trends in fishing reef design and planning. Bull. Mar. Sci. 44: 984–996.
1989

HAUGHTON, M.O. AND K.A. AIKEN, Biological notes on artificial reefs in Jamaican waters. Bull. Mar. Sci. 44: 1033–1037.
1989

HUECKEL, G.J. AND R.M. BUCKLEY, Predicting fish species on artificial reefs using indicator biota from natural reefs. Bull. Mar.Sci. 44: 873–880.
1989

HUECKEL, G.J., R.M. BUCKLEY AND B.L. BENSON, Mitigating rocky habitat loss using artificial reefs. Bull. Mar. Sci. 44: 913–922.
1989

HUNG, E.W.F., Artificial reefs development and management in Malaysia. in: Report of the workshop on artificial reefs development and management, Penang, Malaysia. ASEAN/SF/88/GEN/8: 27–51.
1988

McGURRIN, J.M., R.B. STONE AND R.J. SOUSA, Profiling United States artificial reef development. Bull. Mar. Sci. 44: 1004–1013.
1989

MICLAT, R.I., Artificial reef development – the Philippine experience. In: Report of the workshop on artificial reefs development and management, Penang, Malaysia. ASEAN/SF/88/GEN/8: 63–86.
1988

MILON, J.W., Artificial marine habitat characteristics and participation behavior by sport anglers and
1989 divers. Bull. Mar. Sci. 44: 853–862.

NATIONAL RESEARCH COUNCIL (U.S.), Office of International Affairs, Fisheries technologies
1988 for developing countries: report of an ad hoc panel of the Board on Science and Technology for International Development. National Academy Press. Washington, D.C. 168 pp.

POLOVINA, J.J. AND I. SAKAI, Impacts of artificial reefs on fishery production in Shimamaki,
1989 Japan. Bull. Mar. Sci. 44: 997–1003.

SAMPLES, K.C., Assessing recreational and commercial conflicts over artificial fishery habitat use:
1989 Theory and practice..Bull. Mar. Sci. 44: 844–852.

SAMPLES, K.C. AND J.T. SPROUL. Fish aggregating devices and open-access commercial fisheries:
1985 A theoretical inquiry. Bull. Mar. Sci. 37: 305–317.

SAMPLES, K.C. AND J.T. SPROUL. Fish aggregating devices and open-access commercial fisheries:
1989 for research, technology and management related to artificial aquatic habitats. Bull. Mar. Sci. 44: 527–532.

SINANUWONG, K., Artificial reefs construction Nakornsrithammarat Province. In: Report of the
1988 workshop on artificial reefs development and management, Penang, Malaysia. ASEAN/SF/88/GEN/8: 130–134.

SUNGTHONG, S., Artificial reefs development as a tool for fisheries management in Thailand. In:
1988 Report of the workshop on artificial reefs development and management, Penag, Malaysia. ASEAN/SF/88/GEN/8: 87–91.

YAMANE, T., Status and future plans of artificial reef projects in Japan. Bull. Mar. Sci. 44:
1989 1038–1040.

YOUNG, C., Major artificial reef in WA follows SA lead. Aust. Fish. 47(12): 26–28.
1988

Evaluation of Hatchery Releases of Juveniles to Enhance Rockfish Stocks, with Application to Pacific Ocean Perch *Sebastes alutus**

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Abstract.– The equilibrium contribution of hatchery-released juveniles to a rockfish fishery is evaluated by using a yield-per-recruit model. Hatchery-released juveniles may be worth up to an estimated US$0.16 per juvenile to the fishery. The use of hatchery releases to restore a depleted population of Pacific ocean perch *Sebastes alutus* is examined with the Deriso-Schnute model. This model indicates that hatchery releases have the potential to substantially increase a stock's yield and rate of recovery during the recovery period.

There is a long history of attempts worldwide to enhance marine fisheries by releasing hatchery-reared juveniles. However, few attempts have had long-term success (Yatsuyanagi 1982, Botsford and Hobbs 1984, Isibasi 1984, Ulltang 1984). In theory, hatchery releases can enhance fisheries in two ways. First, juvenile releases can be added to the natural stock on a long-term basis to support a higher level of fishery harvest than that achieved from the natural stock alone. Secondly, juvenile releases can be used on a short-term basis to increase a depleted natural stock more rapidly, then discontinued once the natural stock has recovered.

Pilot releases of the rockfish *Sebastes schlegeli* indicate that large-scale rearing and releases of rockfish may be biologically and technically possible (Sakai et al. 1985, Kusakari In press). The merit of hatchery releases of juveniles for fishery enhancement is examined in the present paper with mathematical models. Specifically, the Beverton and Holt (1966) yield-per-recruit model will be used to evaluate the sustainable increase in fishery catches from a long-term release of hatchery-reared juveniles. The Deriso-Schnute delay-difference age-structure model (Zheng and Walters 1988) will be used to evaluate the fishery benefits from short-term juvenile releases to increase the recovery of depleted rockfish stocks.

Models and methods

To evaluate the equilibrium contribution of hatchery-released juveniles to a rockfish fishery, the Beverton and Holt (1966) equation was used to express the equilibrium yield-per-recruit as a function of the following ratios: instantaneous natural mortality to von Bertalanffy growth (M/K), length at recruitment to asymptotic length, and fishing mortality to natural mortality (F/M) (Beverton and Holt 1966). If a recruit in the yield-per-recruit model is taken to represent a hatchery-released juvenile rather than a recruit from the natural population, then the equilibrium yield per hatchery-released juvenile can be computed from yield-per-recruit tables (Beverton and Holt 1966). Specifically, let Y/R_0 denote the yield per recruit where the recruits are of some reference age, say the age at which they have just become demersal. Then the yield per released fish at age t is just

$$\frac{Y}{R_0}\,e^{Mt}$$

where M is the natural mortality rate from the reference age 0 until release age t. The values of Y/R_0 are tabled as a function of M/K and F/M (Beverton and Holt 1966). The equilibrium yield per hatchery-released juvenile

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Table 1

Von Bertalanffy growth (K), natural mortality (M), M/K, and maximum age for seven commercially important species of rockfish (parameter estimates taken from Pacific Fishery Management Council 1989).

Common name	M/yr	K/yr	M/K	Max. age (yr)
Pacific ocean perch	0.05	0.09	0.56	70+
Yellowtail	0.07	0.16	0.44	64
Shortbelly	0.25	0.21	1.19	12
Widow	0.15–0.20	0.15	1.17*	58
Canary	0.01–0.09	0.16	0.31*	75
Chilipepper	0.20	0.18	1.11	16
Bocaccio	0.25	0.11	2.27	36

*M taken as the midpoint of the range.

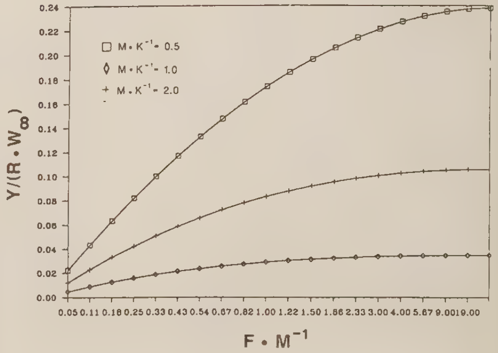

Figure 1

Beverton and Holt yield-per-recruit as a fraction of asymptotic weight at optimum size at entry to the fishery as a function of F/M for three levels of M/K.

will be estimated for values of release age t, M, M/K, and F/M, which are representative estimates for rockfish populations.

To evaluate the short-term releases of hatchery-reared juveniles to restore a depleted rockfish population, a Deriso-Schnute delay-difference age-structure model is used (Zheng and Walters 1988). Deriso (1980) derived a population model that combined simple surplus production models with more detailed age-structure models. Schnute (1985) modified this model with a three-parameter Brody growth model. This Deriso-Schnute model depends on a Brody growth parameter (p), the age of recruitment to a fishery (k), body weights at ages k and k – 1 (W_k and W_{k-1}, respectively), and total annual survival in year t (s_t). Thus, the biomass in year t + 1 ($B_t + 1$) is described as

$$B_{t+1} = (1+p)s_tB_t - ps_ts_{t-1}B_{t-1} + R_{t+1} - ps_t\frac{W_{k-1}}{W_k}R_t,$$

where R_t is the recruitment to the fishery in year t (Schnute 1985). A Ricker stock-recruitment relationship is used to model the recruitment (in weight) from the natural rockfish population and from hatchery-released 1-year-old juveniles to the fishery to obtain the total recruitment (in weight) function (R_t):

$$R_t = AS_{t-k}\exp(-BS_{t-k})\exp(z) + H_{t-k+1}W_k\exp(-M(k-1));$$

where S_t is the spawning biomass, H_t is the number of hatchery-released 1-year-old juveniles, M is natural mortality, and A and B are constants. This model assumes hatchery juveniles are added to the natural population without any density-dependence. The term exp(z) is used to add a stochastic element to the natural recruitment function when the variable z represents a random variable, which has a normal distribution, a mean of 0, and a variance of σ^2. When σ^2 is set to 0, the stochastic term is eliminated, and deterministic recruitment is assumed. The Ricker stock-recruitment relationship appears to represent an appropriate model of recruitment in a natural rockfish population (Archibald et al. 1983).

The Deriso-Schnute model is fit to catch and fishing mortality data for Pacific ocean perch *Sebastes alutus* from Queen Charlotte Sound, Canada, during 1963–77 when the population was fished from an estimated biomass of 82,000 metric tons (t) to 13,000 t (Archibald et al. 1983). The model with its estimated parameters is then used to estimate the equilibrium yield curve to determine the biomass and fishing mortality that achieve maximum sustainable yield (MSY). Then the model with stochastic recruitment is used to simulate the recovery of this depleted stock to the biomass level that supports MSY under several management strategies, including the release of hatchery-reared juveniles.

Results

Values of M for rockfishes typically range from 0.01 to 0.25 per year, K from 0.09 to 0.21 per year, and M/K ratios from 0.44 to 2.27 (Table 1). Values of yield-

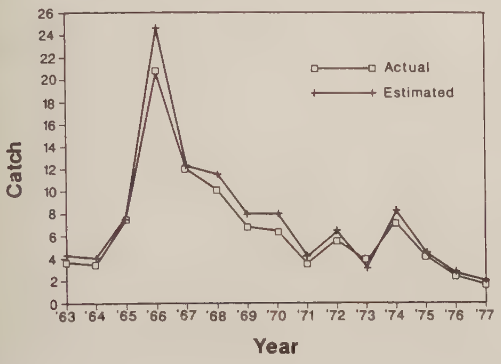

Figure 2

Historic catches (10^3 metric tons) of Pacific ocean perch from Queen Charlotte Sound and estimated catches from the fit of the Deriso-Schnute model, 1963–77.

Table 2

Parameters for the Deriso-Schnute model fit to Pacific ocean perch in Queen Charlotte Sound.

Parameter	Value	Source
Recruitment age (k)	9 years	Archibald et al. (1983)
Natural mortality (m)	0.05 per year	Archibald et al. (1983)
Weight at entry (W_k)	0.614 kg	Archibald et al. (1983)
Weight at age k – 1 (W_{k-1})	0.572 kg	Archibald et al. (1983)
Body growth (p)	0.52 per year	Estimated as mean of range: $1-\sqrt{\frac{W_k}{W_\infty}} \leqslant p \leqslant 1-\frac{W_k}{W_\infty}$
Recruitment model	Ricker	Archibald et al. (1983)
Recruitment parameters A, B	A = 0.29 B = 1.6×10^{-5}	From fit of model to 1963–77 data

per-recruit (expressed as a fraction of the asymptotic weight of the fish, as a function of F/M, and for M/K equaling 0.5, 1.0, and 2.0) are shown in Figure 1. These yield curves assume that the ratio of the length-at-recruitment to the asymptotic length is optimum to achieve maximum yield-per-recruit. For M/K ranging from 0.5 to 2.0, the optimum length at harvest will be 45–86% of the asymptotic length (Beverton and Holt 1966). Thus, in the case of Pacific ocean perch, which has an asymptotic weight of about 1.4 kg, if $M/K = 0.5$, $F/M = 1.0$, and $M = 0.05$ per year, the contribution to the fishery of an individual juvenile released from the hatchery at age 0.25 is calculated as the product of 1.4 kg × 0.17 (from Fig. 1), multiplied by $\exp(0.05 \cdot 0.25)$ or 0.24 kg. The average 1988 ex-vessel price for all rockfishes was US$0.67 per kg (National Marine Fisheries Service 1989); therefore, each 3-month-old, hatchery-released juvenile on the average is worth $0.16 to the fishery. The contribution of a juvenile to the fishery is strongly inversely related to M/K (Fig. 1). For example, if M/K is 1.0 rather than 0.5, then the contribution is only about one-half as much. Also, as long as natural mortality is assumed to be low and constant, changes in the release age have little influence on the contribution of the juvenile to the fishery. However, it is quite possible that natural mortality of young juveniles varies considerably by age and an optimum release age exists, although we have no data to document either case.

Pacific ocean perch in Queen Charlotte Sound, Canada, underwent heavy exploitation from 1963 to 1977 (Fig. 2) (Archibald et al. 1983). A reconstruction of the history of this exploitation by using a catch-at-age model estimates annual exploitable biomass and average fishing mortality during this period (Archibald et al. 1983). The Deriso-Schnute model is fit to the catch history of this fishery during 1963–77 by using estimates of fishing mortality from the catch-at-age model (Fig. 2). All but two of the parameters required for the model are from published values (Table 2). Two parameters (A and B in Table 2) in the stock-recruitment relationship part of the model are estimated by fitting the model to the 1963–77 catch series.

Based on the Deriso-Schnute delay-difference model with the parameters used to fit the catch and effort series (1963–77) and to estimate the equilibrium yield curve, the maximum sustainable yield (MSY) of about 1800 t is achieved at $F_{MSY} = 0.06$ per year (Fig. 3). At that level of F_{MSY}, the corresponding equilibrium biomass (B_{MSY}) is estimated at about 35,000 t. At B_{MSY}, the recruitment of 1-year-old juveniles is estimated at 3.5 million fish, whereas an estimated 1.3 million 1-year-olds recruit if biomass is at the 1977 depleted levels.

Assuming that the goal of restoring the Pacific ocean perch stock is to increase the biomass to 35,000 t so it can be harvested at $F = 0.06$ to achieve MSY, three approaches to stock recovery are examined. One approach has as its goal to increase the biomass to B_{MSY} as quickly as possible by setting F at 0 until the biomass reaches 35,000 t, then the stock will be fished at

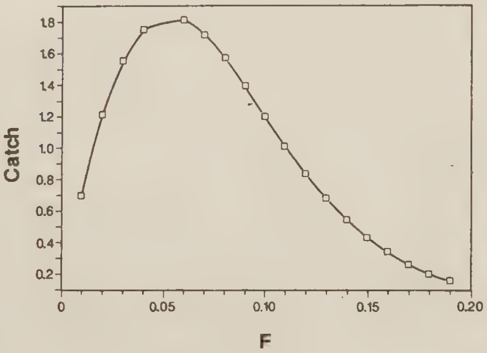

Figure 3
Equilibrium yield curve (10^3 metric tons) for Pacific ocean perch from Queen Charlotte Sound estimated from the Deriso-Schnute model.

F = 0.06. The second approach to stock recovery is to eventually achieve B_{MSY} while also maximizing the yield to the fishery. Under this approach, the stock is fished at F = 0.06 from the beginning. A third strategy, which represents a compromise between these two philosophies, will set F at 0.03 until the biomass reaches 35,000 t, then the stock will be fished at F = 0.06.

Each of these three sequences of F can be evaluated with and without hatchery releases. Catch and biomass series with and without hatchery releases for each sequence of F can be simulated with the stochastic Deriso-Schnute model with the parameters used to fit the population decline. When hatchery releases are used, 5 million 1-year-old juveniles will be stocked annually. This number represents almost four times the natural recruitment for the stock at the 1977 depleted level and about 40% more than the natural recruitment at the B_{MSY} level. The variance of the random variable z in the stochastic recruitment component is assumed to have a variance of 0.3 (Archibald et al. 1983). Based on 100 simulations of each of the six management approaches over 100 years, the mean annual catches, mean cumulative catches and the biomass distributions after 20 years can be computed (Figs. 4–6, Table 3).

When the management strategy closes the stock to fishing to restore it as quickly as possible, B_{MSY} (35,000 t) is achieved in 21 years without stocking and 14 years if 5 million juveniles are stocked annually for 6 years (Table 3). After 20 years, the mean biomass levels are about the same for the stocked and non-stocked cases, so annual catches are about the same and the difference in cumulative yield remains con-

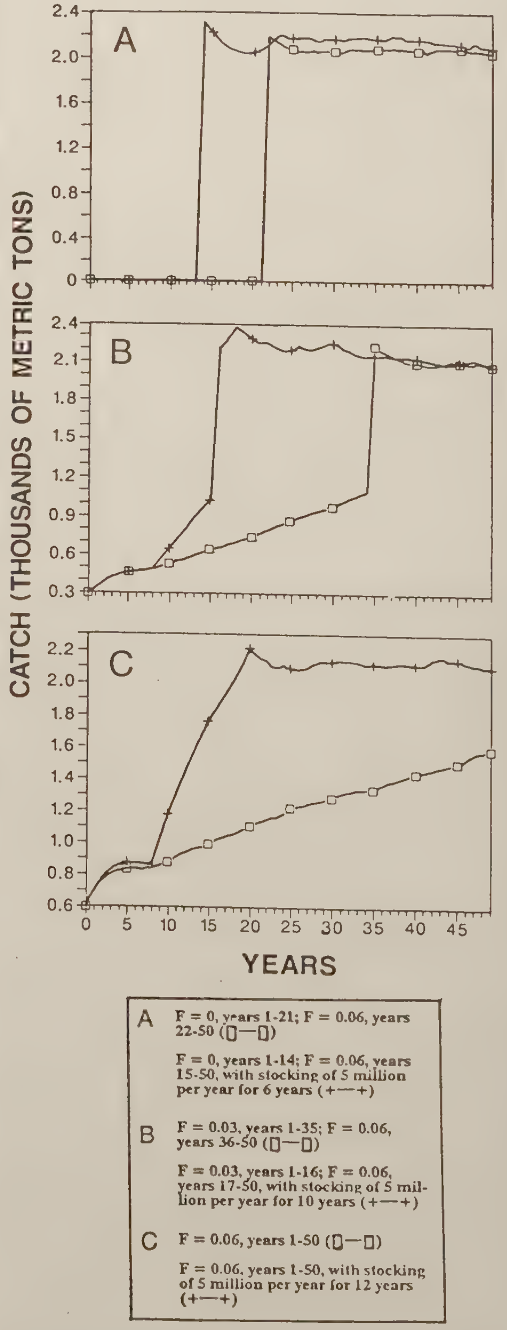

Figure 4
Simulated annual catches of Pacific ocean perch, with and without hatchery releases, for three management strategies.

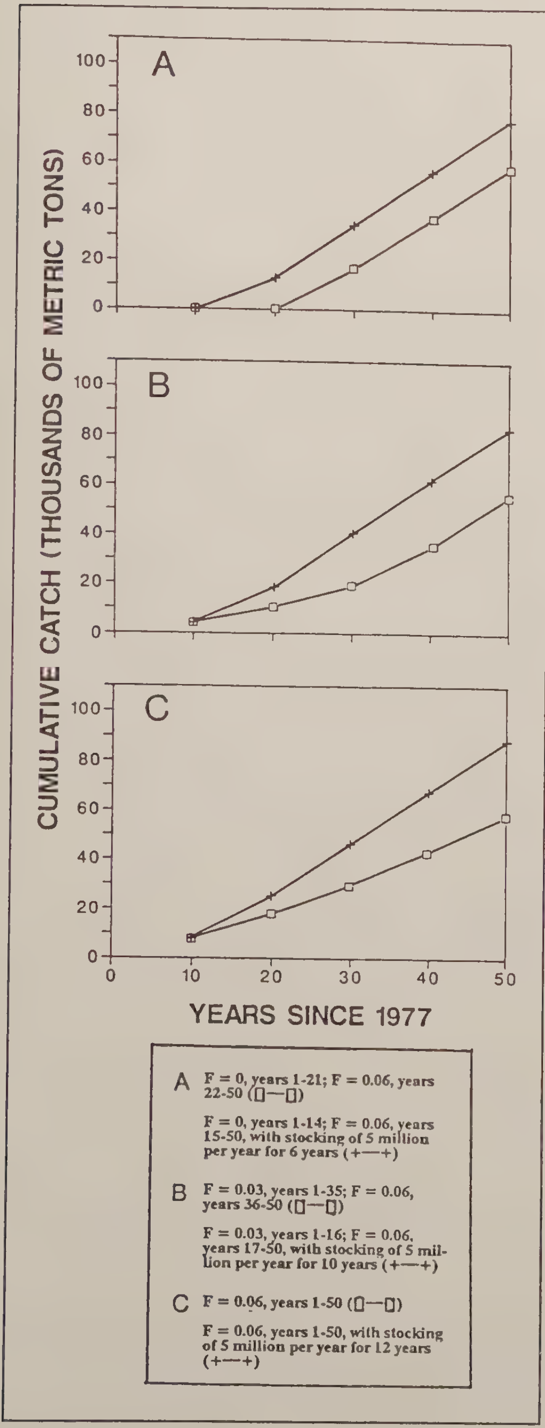

Figure 5
Simulated cumulative catches of Pacific ocean perch, with and without hatchery releases, for three management strategies.

stant (Figs. 4,5). The biomass distributions with and without stocking are very similar after 20 years (Fig. 6).

When F = 0.03, B_{MSY} is achieved in 35 years without stocking and in 17 years when 5 million juveniles are stocked annually for 10 years (Table 3). The annual catches for both the stocked and nonstocked strategies are the same for the first 8 years because of the 8-year lag between the release of juveniles and their entry into the fishery; but beginning in year 9, the annual catches in the stocked strategy exceed those for the nonstocked strategy. In year 16, B_{MSY} is achieved in the stocked strategy, and F is increased to 0.06, which results in a substantial increase in annual catches. The annual catches for the nonstocked strategy lag behind the stocked catches until year 35 when B_{MSY} is achieved and F is increased to 0.06 (Fig. 4). The difference between the cumulative catches for stocked and nonstocked is initially very small, because the two strategies have the same annual catches at the beginning, but the difference grows once the annual catches diverge (Fig. 5). After 20 years, the distribution of biomass for the stocked population is about 10,000 t greater than for the population without stocking (Fig. 6).

When F = 0.06, B_{MSY} is not achieved within 100 years without stocking, whereas B_{MSY} is achieved in 20 years with stocking (Table 3). The patterns of annual and cumulative catches for the stocked and nonstocked cases are similar to the F = 0.03 situation (Figs. 4,5). After 20 years, the distribution of biomass without stocking shows very little change from the level at the beginning of the recovery period, whereas the distribution of the stocked population centers close to B_{MSY} (Fig. 6).

The value of stocking to increase yields while restoring the depleted Pacific ocean perch population can be evaluated by computing the break-even cost of a hatchery-released juvenile based on the increase in cumulative landings. Suppose a hatchery, built and operated by government funds, must meet the economic criterion of a 3% return on investment. Then the break-even cost per juvenile, as a function of *n* years after the start of stocking, can be calculated as follows: (1) Compute the increase in cumulative yield between the comparable stocked and nonstocked strategies, *n* years

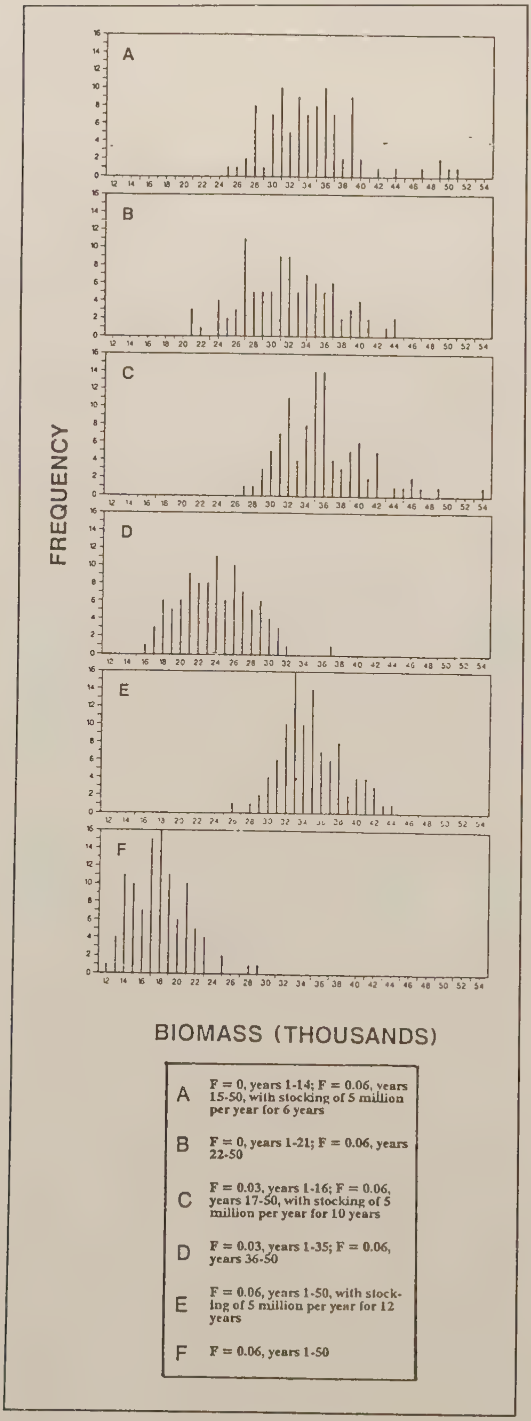

Figure 6

Biomass distributions of Pacific ocean perch 20 years after the onset of hatchery releases (from 100 simulations), with and without stocking, for three management strategies.

after the start of stocking; (2) divide this increase in yield (the result from step 1) by the total number of juveniles stocked to obtain the increase in yield per stocked juvenile; (3) multiply the result of step 2 by the unit value of the yield to the fishery to compute the value to the fishery per stocked juvenile; and, finally, (4) discount this yield cumulated over n years to a present value by dividing the result of step 3 by $(1.03)^n$. Using this approach, based on a wholesale value for Pacific ocean perch of \$0.67 per kg (National Marine Fisheries Service 1989), the break-even cost per juvenile ranges from \$0.04 to \$0.16. For example, under the scenario where the fishery is closed until B_{MSY} is reached, if hatchery juveniles can be stocked at a cost of \$0.16 per juvenile, then hatchery releases result in increasing the value of the catches over the nonstocked strategy equivalent to a 3% annual return on stocking costs for the first 20 years after stocking (Table 4). However, under the scenario where F = 0.06 from the beginning of the recovery period, the break-even cost of a hatchery-released juvenile cannot exceed \$0.04 if the release program is to achieve a 3% annual return over the first 10 years and \$0.08 over a 40-year period.

Looking at just the cumulative yields does not show all of the benefits of stocking, since some of the released juveniles contribute to an increase in standing stock. When the contribution of the released juveniles to both the fishery and standing stock is considered, the relative benefit is the same for all three stocking and harvesting strategies (Table 5).

A delay-difference model very similar to the model used in this analysis, but with a Cushing rather than Ricker recruitment function, has been fit to data on the Pacific ocean perch fishery in waters off Washington and Oregon (Ito et al. 1987). When the Cushing recruitment function is used in our model, the estimates of MSY, F_{MSY} and B_{MSY} change, but the relative contribution of hatchery releases to biomass and yield is unchanged (Table 5). Further, based on simple sensitivity analyses, the relative benefits of hatchery releases by increasing biomass and yield apparently are most sensitive to the ratio of natural mortality to growth (Table 5). Thus, as in the yield-per-recruit model, the relative benefits of hatchery releases are inversely proportional to the ratio of mortality to growth.

Table 3

Catch of Pacific ocean perch cumulated by 10-year periods from the mean of 100 simulations of the Deriso-Schnute model (thousands of metric tons).

Strategy	Years to B_{MSY} (N)	No. of years for which catch is cumulated 10	20	30	40	50
F = 0, years 1–21; F = 0.06, years 11–50	21	0	0	16.8	37.7	58.6
F = 0, years 1–14; F = 0.06, years 15–50, with stocking of 5 million/year for 6 years	14	0	13.0	34.5	56.5	77.9
F = 0.3, years 1–35; F = 0.06, years 36–50	35	4.4	10.6	19.2	35.2	56.2
F = 0.03, years 1–16; F = 0.06, years 17–50, with stocking of 5 million/year for 10 years	16	4.5	18.5	39.7	61.2	82.3
F = 0.06, years 1–50	100+	8.0	17.8	29.8	43.3	58.3
F = 0.06, years 1–50, with stocking of 5 million for 12 years	20	8.3	25.1	46.3	67.5	88.9

Table 4

Break-even cost of hatchery-released juveniles of Pacific ocean perch at a 3% annual rate of return (US$ per juvenile) as a function of years after start of releases.

Strategy	Years 10	20	30	40	50
F = 0, years 1–21; F = 0.06, years 22–50 versus F = 0, years 1–14; F = 0.06, years 15–20, with stocking of 5 million/year for 6 years	0	0.16	0.16	0.12	0.09
F = 0.03, years 1–35; F = 0.06, years 36–50 versus F = 0.03, years 1–16; F = 0.06, years 17–50, with stocking of 5 million/year for 10 years	0	0.06	0.11	0.11	0.08
F = 0.06, years 1–50 versus F = 0.06, years 1–50, with stocking of 5 million/year for 12 years	0	0.04	0.07	0.08	0.07

Table 5

Contribution of juvenile releases of Pacific ocean perch to biomass and cumulative yield 20 years after the start of releases.

Strategy	I Change in biomass per released juvenile (kg/fish)	II Change in yield per released juvenile (kg/fish)	II + III (kg/fish)
A	0	0.43	0.43
B	0.25	0.16	0.41
C	0.31	0.11	0.42
D	0.33	0.08	0.41
E	0.28	0.14	0.42
F	0.18	0.05	0.23
G	0.22	0.26	0.48
H	0.33	0.14	0.47

A: F = 0, years 1–21; F = 0.06, years 22–50 vs. F = 0, years 1–14; F = 0.06, years 15–50, with 5 million juvenile releases for 6 years.
B: F = 0.03, years 1–35; F = 0.06, years 36–50 vs. F = 0.03, years 17–50, with 5 million juvenile releases for 10 years.
C: F = 0.06 vs. F = 0.06, with 5 million juvenile releases for 12 years.
D: F = 0.04 vs. F = 0.04, with 5 million juvenile releases for 12 years.
E: F = 0.08 vs. F = 0.08, with 5 million juvenile releases for 12 years.
F: M = 0.1 instead of M = 0.05 and strategy C.
G: F = 0.08 vs. F = 0.08, with 5 million juvenile releases for 3 years with growth, mortality, and Cushing recruitment model (parameter estimates are from Ito et al. 1987).
H: F = 0.04 vs. F = 0.04, with 5 million juvenile releases for 5 years with growth, mortality, and Cushing recruitment model (parameter estimates are from Ito et al. 1987).

Discussion

The Beverton and Holt (1966) model provides a simple means of evaluating the equilibrium contribution of a long-term hatchery release program to the fishery. The model shows that if M/K is 0.5 for the hatchery-released juveniles from the time of release to capture in the fishery, and if the cost of each released juvenile is less than US$0.16, its value to the fishery exceeds its cost. The length-at-entry for fish in these analyses is assumed to be the length that maximizes the yield-per-recruit, that is, 45–86% of the asymptotic length. If the length-at-entry to the fishery is below this level, as with some long-lived, slow-growing fishes, the contribution of the hatchery releases to the fishery will be less than the value calculated by the model. However, the yield-per-recruit surface is relatively flat, so unless the length-at-entry is widely different from the optimum length, the reduction in the contribution of the hatchery releases should not exceed 10–15% of the value corresponding to the optimum length-at-entry (Beverton and Holt 1966). The results of the model are particularly sensitive to levels of M/K, asymptotic weight, and market price. Interestingly, the results depend only on the ratio of M to K, and the slow growth of rockfish does not have a bearing on the equilibrium benefit of the released juveniles. Three commercially important species—Pacific ocean perch, yellowtail rockfish *Sebastes flavidus*, and canary rockfish *S. pinniger*—have M/K values around 0.5 and, from a population dynamics standpoint, offer the most potential for hatchery releases (Table 1).

Based on the Deriso-Schnute model, the level of F_{MSY} for Pacific ocean perch in Queen Charlotte Sound is estimated at 0.06 per year. This value is consistent with the finding of Archibald et al. (1983) and considerably less than the F levels of 0.2–0.5 per year during the depletion of the stock. Given the slow growth and long lag between spawning and recruitment to the fishery, stock recovery for rockfish is a long-term process. Fishery managers must decide whether the goal of the recovery program is to return the stock to B_{MSY} as quickly as possible or to follow a more gradual return while allowing fishing. Under both approaches, stocking reduces the time to reach B_{MSY} and increases the yield to the fishery. Both benefits must be considered in evaluating the merits of a hatchery-release program for stock recovery. As with the yield-per-recruit analysis, Pacific ocean perch, yellowtail rockfish, and canary rockfish are the three commercial species, based on their low M/K ratios, that offer the most potential for stock recovery with hatchery releases (Table 1).

Based on population-dynamics considerations, the use of hatchery releases for fishery enhancement appears to have merit for certain species of rockfishes. However, population dynamics represents only one part of the post-release ecology, and a fuller understanding of this ecology is necessary to predict the success of hatchery releases. For example, hatchery-reared Kuruma prawns *Penaeus japonicus* were released in a number of similar locations around Japan (Isibasi 1984). Increases in catches were documented in some instances, but no changes were evident in many others; researchers generally were unable to explain this variation (Isibasi 1984). While this analysis assumes that large-scale hatchery releases are possible, no such releases have been done, and nothing is known of the economics of a rockfish hatchery. Further, hatchery-released juveniles have been assumed to have the same behavior and natural mortality as wild stock. This may be an overly optimistic assumption because pilot hatchery releases for other species often have higher and more variable natural mortality than is thought to occur in wild stock (Kyokai 1983).

Citations

Archibald, C.P., D. Fournier, and B.M. Leaman
1983 Reconstruction of stock history and development of rehabilitation strategies for Pacific ocean perch in Queen Charlotte Sound, Canada. N. Am. J. Fish. Manage. 3:283–294.

Beverton, R.J.H., and S.J. Holt
1966 Manual of methods for fish stock assessment. Part II - Tables of yield functions. FAO Fish. Tech. Pap. 38 (Rev. 1), 67 p.

Botsford, L.W., and R.C. Hobbs
1984 Optimal fishery policy with artificial enhancement through stocking: California's white sturgeon as an example. Ecol. Modell. 23:293–312.

Deriso, R.B.
1980 Harvesting strategies and parameter estimation for an age-structured model. Can. J. Fish. Aquat. Sci. 37:268–282.

Isibasi, K.
1984 A statistical assessment on the effect of liberation of larvae in the sea farming—I. On the effect of liberation in the case of Kuruma prawn (*Penaeus japonicus*). Bull. Tokai Reg. Fish. Res. Lab. 113:141–155.

Ito, D.H., D.K. Kimura, and M.E. Wilkins
1987 Status and future prospects for the Pacific ocean perch resource in waters off Washington and Oregon as assessed in 1986. NOAA Tech. Memo. NMFS-F/NWC-113, Northwest & Alaska Fish. Sci. Cent., 7600 Sand Point Way NE, Seattle 98115, 50 p.

Kusakari, M.
In press Mariculture of kurosoi, *Sebastes schlegeli*. Environ. Biol. Fish.

Kyokai, S. (editor)
1983 Tsukuru gyogyo. Norin Tokei Kyokai (Agric. For. Stat. Assoc.), 753 p. [in Jpn., Engl. transl. of Table of Contents only by T. Otsu, 1987; full translation avail. from JJP].

National Marine Fisheries Service
1989 Fisheries of the United States, 1988. U.S. Natl. Mar. Fish. Serv. Curr. Fish. Stat. 8800, 116 p.

Pacific Fishery Management Council
1989 Pacific coast groundfish fishery management plan, draft amendment 4. Pac. Fish. Manage. Counc., Portland, OR, 52 p.

Sakai, K., H. Nagashima, and K. Kiso
1985 Growth and movement of artificially reared young rockfish, *Sebastes schlegeli*, after release in Matsushima Bay. Bull. Tohoku Reg. Fish. Res. Lab. 47:21–32 [in Jpn., Engl. abstr; Engl. transl. 125 by W.G. Van Campen, 1988, 19 p., avail. Honolulu Lab., Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396].

Schnute, J.
1985 A general theory for analysis of catch and effort data. Can. J. Fish. Aquat. Sci. 42:414–429.

Ulltang, O.
1984 The management of cod stocks with special reference to growth and recruitment overfishing and the question whether artificial propagation can help to solve management problems. *In* Dahl, E., D.S. Danielssen, E. Moksness, and P. Solemdal (eds.), The propagation of cod *Gadus morhua* L., p. 795–817. Flødevigen rapp., 1.

Yatsuyanagi, K.
1982 Productive effect in stocking of prawn seedling in waters adjacent to Yamaguchi Pref. and Suho-Nada. Bull. Yamaguchi Prefect. Naikai Fish. Exp. Stn. 10:1–52.

Zheng, J., and C.J. Walters
1988 Population dynamics and stock assessment of Wanshan Spring *Decapterus maruadsi* (T.&S.) in South China Sea. Fish. Res. (Amst.) 6:217–231.

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5

Fisheries Applications and Biological Impacts of Artificial Habitats

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This chapter examines many of the applications of artificial habitats in various aquatic environments. The particular focus is on their biological impacts with reference to fisheries and their actual or possible role in fishery management.

Grouping artificial habitats by their primary users is a useful way to categorize the applications of these structures for analysis. Four principal categories recognized here include artisanal fisheries; small-scale commercial fisheries; recreational fisheries and diving; the replacement of habitat lost from shoreside development (mitigation); and enhancement of habitat in marine reserves. Examples of the uses and impacts of artificial habitats for these categories are discussed in the first section of this chapter.

The second section focuses on the biological impacts of artificial habitats. Their much debated role in aggregating production and creating new production is presented in a broader context. It is proposed that artificial habitats may (1) redistribute exploitable biomass without increasing it or total stock size; (2) aggregate previously unexploited biomass and increase exploitable biomass; or (3) increase total biomass. The discussion of each provides examples. Throughout the text, attention is given to identifying the effective uses of artificial habitats in fishery management.

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I. Applications

Some of the better documented fishery and environmental applications of artificial habitats are presented in this section. The intent is not to provide an exhaustive global review, but rather to provide illustrative data for representative situations. This augments the description and synopsis provided in Chapters 1 and 2.

A. Artisanal Fisheries

Artisanal fishermen have developed many artificial reef and fish-aggregating device (FAD) designs to create fishing grounds close to their villages. Such structures traditionally have been constructed with materials of opportunity, for example, sticks, poles, bamboo, or bundles of brush, but are also frequently made from concrete and scrap tires.

In the Philippines, a widely used artificial reef module is made from bamboo poles arranged in a tripod, weighted with stones, and covered with coconut palm fronds (Fig. 5.1). The units are usually placed in calm, shallow coastal water. When such artificial habitats are used in deeper water, a FAD may be attached to mark their location and to attract pelagic fishes. Large-scale deployments of reefs and FADs are used in regional development programs (Fig. 5.2).

Approximately 16,000 pyramid bamboo modules in clusters of 50 have been set along 40 km of Philippines coastline in the central Visayan Islands, and over 8000 bamboo modules have been deployed in the Samar Sea-Ticao Pass Project (Miclat, 1988). These artificial habitats are planned, constructed, deployed, and maintained by the village fishermen (Miclat, 1988). The reefs are conveniently located, and the value of the catches during the first year of deployment can exceed the cost of the reefs and their installation (Miclat, 1988). Catches include caesionids, mullids, lutjanids, serranids, siganids, lethrinids, haemulids, acanthurids, and apogonids (Miclat, 1988). The bamboo pyramids used in the Central Visayan Project had an estimated installed cost of U.S. \$4.00/m^3 and annual harvests of 8 kg/m^3; therefore, if all of the fish caught were sold, the installed cost of the reef would be recouped in nine months (Bojos and Vande Vusse, 1988). Recently, artificial reefs made from concrete reinforced with bamboo have been used instead of bamboo, which only has a 4-yr life span (Bojos and Vande Vusse, 1988).

Although FADs are used by artisanal fishermen in many countries, the situation in the Philippines is unique. The approximately 3000 FADs owned and deployed by commercial tuna purse seiners are also used by artisanal fishermen who handline around the FADs for large tunas (yellowfin, *Thunnus albacares*) swimming too deep to be caught in purse seine nets (Aprieto,

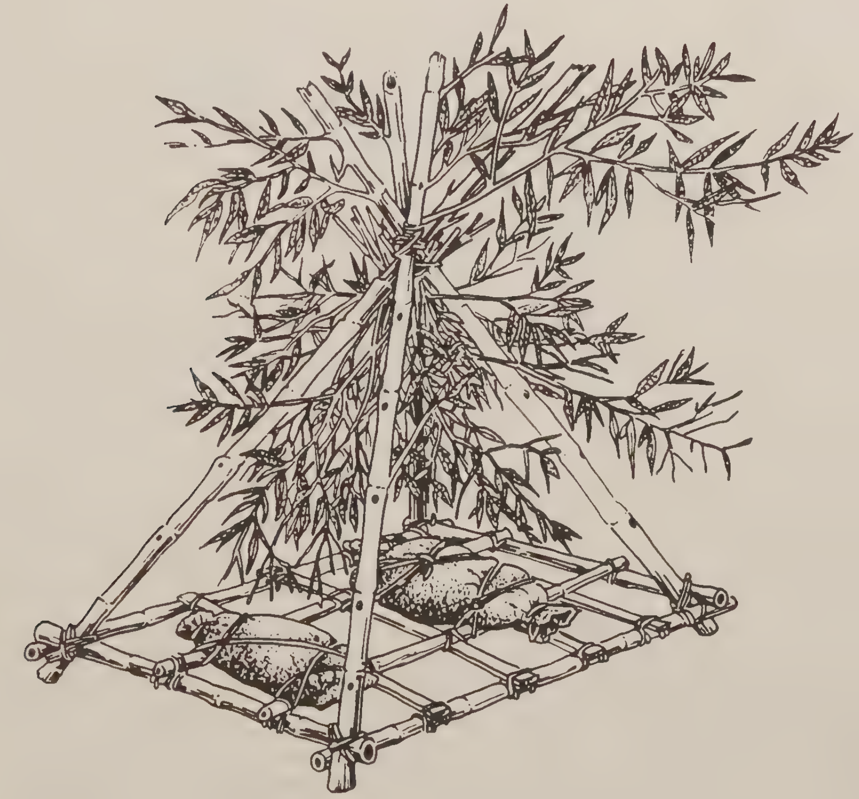

Figure 5.1 A benthic artificial reef used in the Philippines (redrawn from Aprieto, 1988).

1988). Because they exploit different resources and appropriate accommodations exist between commercial and artisanal fishermen, fisheries conflicts between these two user groups are rare.

In Cuba and Mexico artisanal fishermen use artificial reefs to attract lobster (*Panulirus argus*) and to facilitate their capture. In Cuba, flat layers of mangrove branches are used to form shelters (about 2 m in length and 2 m in width) that are set in depths of 4–6 m and raised about 10–15 cm above the ocean bottom by cross branches (Fig. 5.3). Fishermen shake the shelters and net the escaping lobsters. In the Gulf of Batabano, Cuba, cooperatives use 120,000 lobster shelters and harvest about 7000 metric tons (t) of lobster (U.S. National Research Council, 1988). In Mexico, similar shelters have been used since the late 1960s; many are now made from ferroconcrete and corrugated roofing material.

Thailand's Department of Fisheries has used old tires and concrete cubes

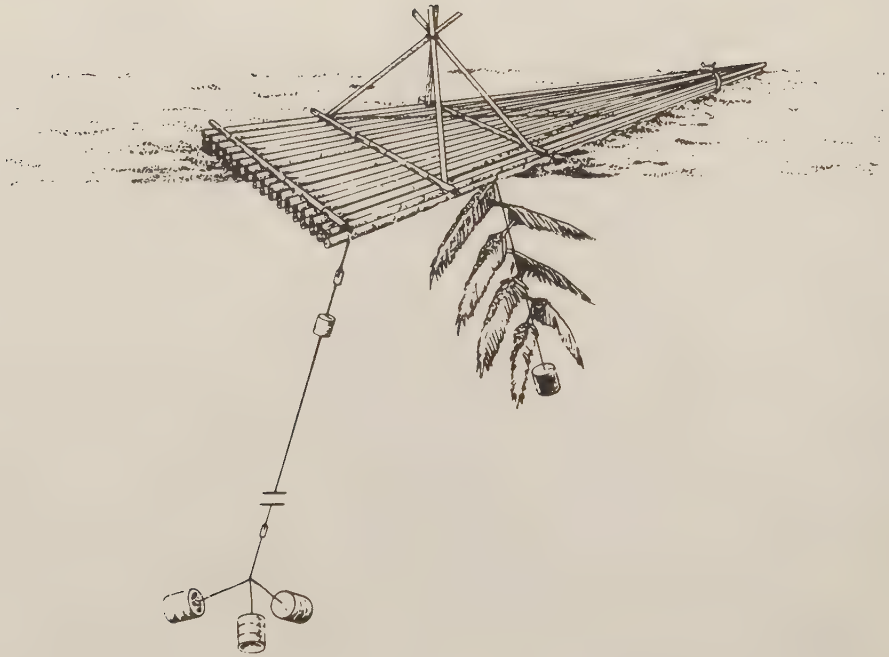

Figure 5.2 A bamboo raft or payao is a FAD used for tuna in the Philippines (redrawn from Aprieto, 1988).

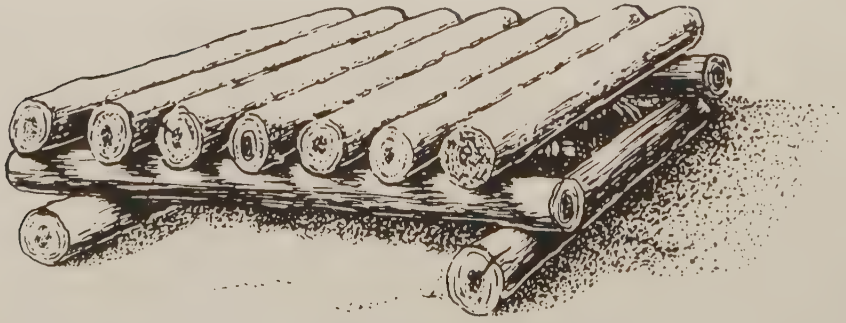

Figure 5.3 A traditional Cuban lobster shelter (after U.S. National Research Council, 1988).

to construct artificial reefs for artisanal fishermen in the Gulf of Thailand. These reefs, placed on soft-bottom areas, provide hard substrata and vertical relief that attract valuable snappers (Lutjanidae) and groupers (Serranidae) normally not found at soft-bottom sites. In one application, the reefs were seeded with green mussels (U.S. National Research Council, 1988).

In another application, 2805 concrete cylinders were deployed in the Gulf of Thailand over a 41 km^2 area previously used by trawlers and village fishermen as a fishing ground for threadfin (*Eleuteronemus tetradactylum*, family Polynemidae). This artificial reef had the effect of closing the area to trawlers, thus allocating the resource to village fishermen using gill nets from small vessels (Sinanuwong, 1988). Before the deployment of this artificial habitat, village fishermen fished this resource for about 15 days in late November and early December, before the schools were depleted by trawlers and push-netters. However, after deployment, trawlers and push-netters were unable to operate in the area, and village fishermen were able to fish the schools for at least 6 months. The threadfin catch by village fishermen was 1746 kg (average catch rate, 4.7 kg/trip) before deployment and 5562 kg (average catch rate, 8.3 kg/trip) after deployment (Sinanuwong, 1988). Unfortunately, the substrata where the reefs were deployed were soft, and most of the reefs sank into the bottom sediment after about a year.

The Thai government is considering plans to increase its artificial reefs by using concrete cube modules (volumes of 1 and 2 m^3) to construct large artificial reefs with volumes of 25,000–50,000 m^3 and covering areas of 50–100 km^2 (Sungthong, 1988). These large reefs would close large areas to trawling and create fishing sites for artisanal fishermen.

By 1988, the Malaysian Department of Fisheries artificial habitat program had deployed 65 artificial reefs made from over 505,000 scrap tires, seven reefs made from sunken ships, and four reefs made from pyramids of concrete pipes (Hung, 1988). The tire reefs consist of modules of tires tied into pyramids with polyethylene rope. The number of tires per artificial reef site varied: most of the reefs (40%) had fewer than 1000 tires, but a few (5%) were composed of more than 30,000 tires (Hung, 1988). The objective is to enhance biological productivity and fishery resources in coastal waters. To prevent overfishing of resources aggregated at the artificial reefs, the Department of Fisheries prohibits fishing within 1.7 km of the artificial reefs (Hung, 1988). By 1990 the artificial reefs are expected to contain a total of two million tires.

B. Small-Vessel Commercial Fisheries

Small-vessel commercial fishermen typically use larger vessels with greater fishing power, hydraulics, depth finders, and inboard engines, than do artisanal fishermen. In many developed countries, they operate at marginal economic levels, and governments perceive programs of construction and deployment of artificial habitats as being beneficial to the financial operations of these fisheries.

Japan has the most extensive system of artificial reefs to assist the small-vessel commercial fishermen of any nation, as described in detail in Chapter 2. Since 1976, the Japanese government has spent over U.S. $1 billion for reefs with an enclosed volume exceeding 17 million m^3 (Grove *et al.*, 1989), so that 9.3% of total nearshore seafloor to a depth of 200 m is covered with artificial reefs (Yamane, 1989). (See numerous illustrations in Chapter 4.)

The Japanese artificial reefs reportedly are popular with fishermen because they increase catches for a wide range of both demersal and pelagic fishes and decrease operating costs (Yamane, 1989). Whether the reefs actually increase fishery catches has been addressed by Polovina and Sakai (1989), who analyzed the 1945 to 1985 catch at a small bay in Hokkaido, Japan, where 50,000 m^3 of artificial reefs were deployed from 1960 to 1985. They found that although several resources were caught, an increase in landings for only one resource could be attributed to the artificial reefs: catches of octopus (*Octopus dofleini*) increased by an estimated 1.8 kg/m^3 of artificial reef. Fifty-three percent of the fishermen surveyed from this bay used the artificial reefs regularly, 12% used them only when fishing elsewhere was poor, and 36% did not use them at all (Polovina and Sakai, 1989). Further, 33% of these fishermen thought the reefs had expanded the amount of productive habitat, 38% thought the reefs did not increase the productive habitat, and 30% were unable to decide about this question.

In the Mediterranean Sea, Italy, France, and Spain have modest artificial reef and FAD development projects. The coastal environment in many parts of the Mediterranean Sea has a soft bottom, water with a high nutrient level that is not fully recycled by the ecosystem, and many nearshore fisheries that are overfished, in part, because of illegal trawling. The objectives of the projects include (1) protection of nursery grounds from illegal trawling, (2) attraction of pelagic and benthic species that use hard substrata, and (3) provision of substrata for shellfish farming and nutrient recycling in eutrophic environments. Initially, various materials including car bodies and ships were used as artificial reefs, but most recent and planned artificial reefs consist of concrete cubes or blocks (see Figs. 2.2 and 2.3).

In Italy, Bombace (1989) found that a concrete reef of 4300 m^3 increased both mussel and fish catches including striped mullet (*Mullus barbatus*), meagre (*Arnyrosoma regius*), sea bass (*Dicentrarchus labrax*), and mussels (*Mytilus galloprovincialis*). The net proceeds for a fisherman operating within the reef were 2.5 times greater than those operating outside the reef. In eutrophic waters such as those of the Adriatic, the cost of the reefs was recovered about three times in seven years (Bombace, 1989). Initially, trawlers were opposed to the reefs because the area was closed to trawling, but their attitude changed as their catches increased along the edges of the reef zone (Bombace, 1989).

When artificial reefs are deployed in Italy, the area covered by reefs typically is designated as a marine zone, and activities and users in it are regulated. However, the demands to harvest resources in these zones often exceed their productivity, and administrators are faced with the challenge of allocating resources among users (Bombace, 1989). Commercial fishermen in Italy are promoting the development of more marine zones protected by artificial reefs; France has less interest in developing new zones, and Spain is just beginning to evaluate artificial reefs (Bombace, 1989).

Insular nations also have deployed artificial reefs and FADs to assist commercial fishermen. For example, 19 areas around Taiwan have artificial reefs built from concrete blocks deployed in 20–40 m depths on flat, sandy, or pebble bottoms to improve fishing sites (Chang, 1985). In Jamaica, artificial reefs made from scrap tires weighted with rocks or concrete are used to create fishing grounds near fishing villages and to provide habitat in areas closed to fishing to protect spawning stock from overfishing (Haughton and Aiken, 1989).

Most South Pacific island governments use FADs widely to enhance catches of offshore pelagic fishes (Fig. 5.4). Evaluation of FADs in American Samoa showed that their use could significantly increase catch per unit effort (CPUE) of offshore pelagic fishes for a troll fishery (Buckley *et al.*, 1989). However, replacing lost FADs is a permanent task for fishery departments since the life span of FADs anchored in unprotected ocean around Pacific islands is often only a few years. Further, FADs do not always increase catches significantly; a study in Puerto Rico found only a slight increase in catches with FADs (Feigenbaum *et al.*, 1989).

Increased CPUE due to artificial reefs and FADs alone may not justify their use by commercial fishermen when they receive heavy and unregulated usage. Since artificial reefs and FADs are usually located in accessible sites, they produce increases in fishing effort, possibly increase the catchability of the gear, and hence increase fishing mortality. Concern has been expressed that even for pelagics, overfishing may occur as a result of the increase in fishing mortality (catch) arising from the use of FADs (Floyd and Pauly, 1984). However, even if artificial reefs and FADs do not have a detrimental impact on the exploited stocks, they still may not be beneficial economically. An economic study of commercial open-access fisheries around FADs in Hawaii found that even if high levels of fishing at FADs do not result in recruitment overfishing, and if fishing effort is unregulated, installation of FAD networks will not generally increase fishermen's aggregate

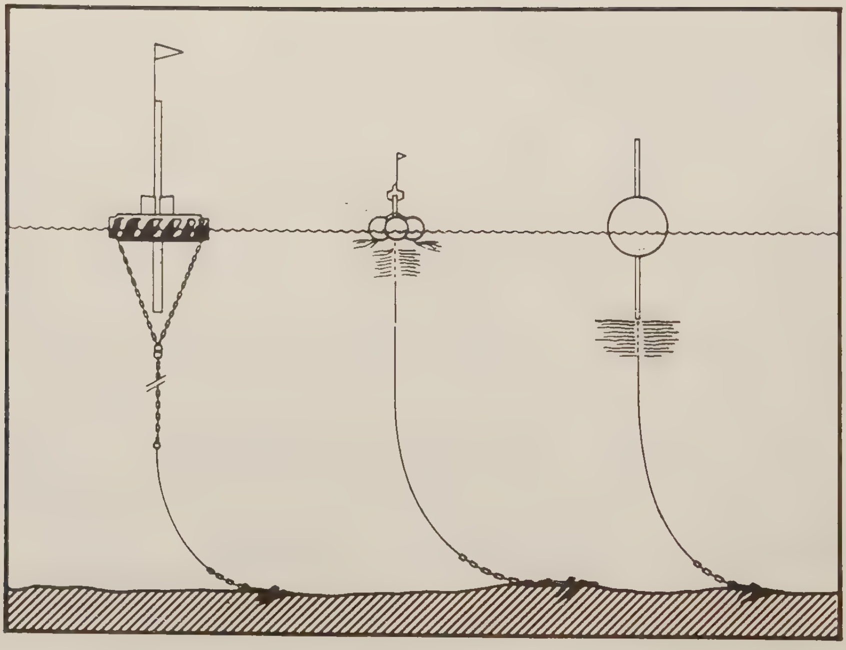

Figure 5.4 Representative FADs used in the Pacific Ocean (redrawn from U.S. National Research Council, 1988).

profit (Samples and Sproul, 1985). Further, deployment of FADs could result in decreases in employment, harvest levels, and sustained gross revenues. Limiting the commercial fishing effort at FADs is seen as a means of preventing these detrimental impacts (Samples and Sproul, 1985).

C. Recreational Fishing and Diving

Artificial reefs and FADs also are popular with recreational fishermen and divers because they provide convenient sites with a concentration of fishes and other organisms. Although globally they are not as widespread as artisanal and commercial fishing applications, where artificial habitats are employed recreationally, use can be extremely intensive. They often are constructed and deployed by sport fishing and diving organizations and state fishery departments in freshwater and marine settings. The most common materials used are ships, concrete, tires, and stone rubble (McGurrin *et al.*, 1989).

The most widespread recreational usage is in the United States. In the Gulf of Mexico, for example, 4000 petroleum structures function as artificial reefs (McGurrin *et al.*, 1989). Even while these structures are producing gas and oil, they are heavily used by recreational fishermen and SCUBA divers (Reggio, 1989). Louisiana has 3100 petroleum structures, which are the destinations of about 37% of all saltwater recreational trips, and over 70% of all recreational trips more than three miles offshore (Stanley and Wilson, 1989). A survey in southern Florida found that about 28% of the recreational fishermen and 14% of the sport divers regularly used artificial reef sites (Milon, 1989). Brush, timbers, tires, rocks, and concrete materials are used in lakes and reservoirs to enhance fishing (D'Itri, 1985). A large artificial reef covering 9500 m^2 was constructed in Smith Mountain Lake, Virginia, with 7000 scrap tires and 400 Christmas trees (Prince *et al.*, 1985). Sunfishes (*Lepomis* spp.) and white catfish (*Ictalurus catus*) were more abundant at this artificial reef site after deployment of reef materials. Furthermore, fishes foraged on the artificial reefs and catfishes deposited eggs inside the artificial reef (Prince *et al.*, 1985). A more detailed review of U.S. sport fishing habitats is provided in Chapter 2.

State government agencies in Australia also support artificial reefs for recreational fishing and diving. One structure is made of tires assembled in a tetrahedron to create fishing and diving sites, which are closed to professional fishermen (Young, 1988). In one instance, 34,000 tires, at a cost of A $205,000, were deployed on the premise that the artificial habitat would increase revenues in the local community through increased spending by sport fishing and diving interests (Young, 1988).

The reefs and FADs concentrate both fish and fishermen. Some concerns over the resource and the conflicts between users have been raised by Samples (1989) and others. Two forms of conflicts, i.e., competition over a common stock and conflicts from user congestion, have been observed (Samples, 1989). An example of the former occurs between commercial pole-and-line boats and recreational trollers around FADs in Hawaii. A pole-and-line vessel can capture all of the skipjack tuna (*Katsuwonus pelamis*) around a FAD, leaving nothing for recreational trollers in the short term.

Also, conflicts due to user congestion occur when many users are concentrated around a reef or FAD, often with various types of gear, such as purse seiners and trollers or handlining and diving gear. A number of approaches that restrict access, limit effort, or segregate users in space and time may resolve these conflicts (Samples, 1989). Of course, carefully planned artificial reefs and FADs also can serve to shift effort away from heavily used natural sites. Broader aspects of fishery management are discussed more fully in Chapter 7.

Artificial reefs for recreational uses have been constructed and deployed by fishing and diving clubs, which, unfortunately, may lack the resources or inclination to properly research the siting, design, and materials. Experience in Florida and other states indicates that the structures may be ineffective and even damaging (Andree, 1988). Andree (1988) has recommended that a Florida artificial reef plan be developed to establish standards for siting, design, and materials, and to establish central artificial reef permitting, maintenance, and monitoring systems. As other areas of the world initiate such programs, the experiences in active artificial habitat sites need to be consulted to avoid mistakes and negative environmental impacts.

D. Environmental Mitigation and Enhancement

Applications of artificial reefs (for uses other than increasing fishing success) include providing habitat to mitigate its loss due to coastal development or pollution and to improve habitat in marine reserves. This is a relatively recent application of this field, and much of the experience is limited to the Pacific mainland coast of the United States. In southern California, for example, the San Onofre nuclear station has affected organisms in two ways: by killing larval, juvenile, and adult fishes that are taken into the plant with the cooling water, and by producing a turbid plume that affects kelp, fishes, and invertebrates in the San Onofre kelp bed. A 120 ha artificial reef has been proposed as in-kind mitigation for impacts to the kelp-forest community from the plume, and a 60 ha structure proposed as out-of-kind mitigation for egg, larvae, and juvenile fish mortality from entrainment (Ambrose, 1990).

Loss of rocky habitat due to near shore filling was successfully mitigated with a 2.83 ha quarry rock artificial reef in Puget Sound, Washington (Hueckel *et al.*, 1989). An important feature of this mitigation was that before a site for the habitat was selected, a set of benthic species was identified to predict colonization of the site by economically important fish species.

On the Pacific coast of Costa Rica, 5000 scrap tires were used to construct new habitat to protect marine fauna rather than for fishing (Campos and Gamboa, 1989). The reef, used by juvenile and adult fishes, was not marked, apparently to prevent fishermen from finding and fishing the area. Artificial reefs may have potential to protect or improve aquatic ecosystems. For example, in Maryland's Chesapeake Bay artificial reefs have been proposed to provide habitat for the American oyster (*Crassostrea virginica*) to restore oyster population levels, not for fishery harvest, but to filter excessive nutrient and particulate levels from the water (Myatt and Myatt, 1990).

In the case of mitigation, it is important to be sure that the artificial reefs are an appropriate habitat, are properly sited to replace the lost habitat, and are not adversely impacting other species. For example, species that use flat, or low-relief habitat may be adversely impacted if high-profile materials are deployed.

II. Biological Impacts

A considerable body of literature deals with the ecology at artificial habitat sites (see Chapter 3), whereas few studies address the biological impacts of artificial reefs and FADs on fish populations (Bohnsack and Sutherland, 1985; Bohnsack, 1989). The limited number of studies of this latter aspect is certainly not due to a lack of interest but rather to the difficulty in collecting the appropriate data. Data must be collected from large-scale applications of artificial habitat on an appropriate spatio-temporal scale to determine the possible biological impacts of artificial habitat in the presence of variations in the environment, fishing strategies, and gear. The scale of most research or pilot applications of artificial habitat is too small to detect biological impacts on stocks, even at a local level. Thus, much of the current thinking on the biological impacts of artificial habitat tends to be speculative. (The reader may consult Chapter 6 for a review of ecological assessment methods.)

Often discussions on the impacts of artificial reefs and FADs distinguish between impacts due to aggregation and those due to "new production" (Bohnsack, 1989). However, from both a management and biological perspective, it is important to make the distinction between aggregation that simply redistributes exploitable biomass and aggregation that attracts biomass not previously exploited, while increasing the exploitable biomass. It is useful to consider the three types of impacts on the exploitable biomass and the total stock due to the artificial habitat:

- Artificial reefs and FADs can simply redistribute the exploitable biomass without increasing it or total stock size;
- They can aggregate previously unexploited biomass and increase the exploitable biomass but not the total stock size;
- When stocks are limited by high-relief habitat, artificial reefs can increase stock and hence, total stock size.

These three types of impacts, therefore, distinguish between not only the two types of aggregation but also total stock size and exploitable biomass. Because some of their biological aspects will differ, the three impacts are discussed separately in subsequent sections. However, all three may occur in varying degrees in any artificial habitat application. They are illustrated in Fig. 5.5.

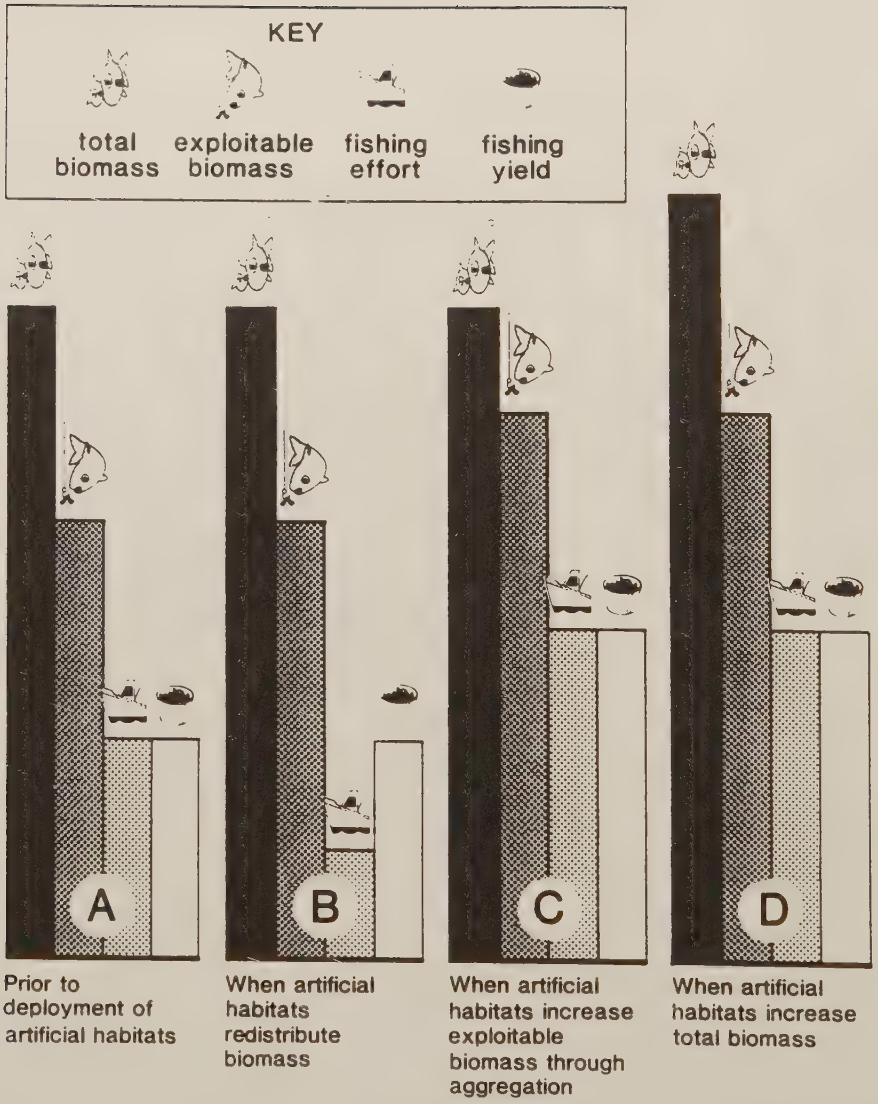

Figure 5.5 Three possible impacts of artificial habitat. (A) Total biomass, exploitable biomass, fishing effort, and yield for a resource prior to deployment of artificial habitats. Note the catch rate (yield:effort) is 1.0, and the yield is about one third of the total biomass. (B) When artificial habitats just redistribute the exploitable biomass to make it easier to catch, the same catch can be obtained with lower effort. (C) When artificial habitats increase the exploitable biomass but not the total biomass, an increase in catch can be achieved with greater effort without a reduction in catch rate, assuming that recruitment overfishing does not occur. (D) When artificial habitats increase the total biomass, the levels of all the variables in part (A) increase. Note that the only difference between (C) and (D) is the increase in total biomass.

A. Impacts Due to a Redistribution of Exploitable Biomass

For some resources, artificial habitat may primarily change the distribution of the exploitable biomass without increasing it or the total stock (Fig. 5.5 part B). For example, some of the resources exploited in the natural habitat move to the artificial habitat, or a highly mobile resource that moves between natural habitats may visit artificial habitats as well.

This type of impact appears to be illustrated by flatfishes (Pleuronectidae) in the study by Polovina and Sakai (1989) on the impacts of 50,000 m^3 of artificial reefs deployed in Shimamaki Bay off Hokkaido, Japan. Despite the flatfishes representing an estimated 30% of the gill-net catches at the artificial reefs, no increase in flatfish landings could be attributed to the reefs when landings from the entire bay were considered (Polovina and Sakai, 1989). In sonic tagging experiments, flatfishes readily moved from natural habitat to artificial reefs, but they were not long-term residents at either site (Kakimoto, 1984). Polovina and Sakai (1989) concluded that the artificial reefs redistributed the flatfishes but did not change their exploitable biomass.

Although the Shimamaki study did not identify any biological impacts from the redistribution of exploitable biomass, there are potential impacts caused by artificial reefs that redistribute exploitable biomass. The greatest potential impact may be a reduction in exploitable biomass if fishing at the artificial habitat is not restricted. Siting of artificial habitats usually allows them to be more accessible to fishermen all year and often works to support a higher density of fishes than a natural habitat. The higher density may increase catchability of the fishing gear, and the greater accessibility increases fishing efforts, which can result in higher fishing mortality. An increase in fishing mortality will decrease exploitable biomass in the area. Whether this decrease results in lower catches or recruitment to the fishery, either locally or in an adjacent region, depends on the stock dynamics. If the stock is migratory, then heavy fishing mortality in one region will result in lower levels of exploitable biomass in adjacent regions. If a strong regional stock–recruitment relationship exists, then heavy local fishing mortality could reduce future recruitment.

Similar to the situation in Shimamaki Bay, application of artificial reefs in the Gulf of Thailand also did not appear to increase the exploitable biomass for one resource. However, the allocation of the resource among user groups was altered (Sinanuwong, 1988). The reef site in the Gulf of Thailand was closed to trawlers and push-netters, and the threadfin resource was allocated to small-vessel, village fishermen using gill nets (Sinanuwong, 1988). Village fishermen had previously fished this resource for a short time until the schools were depleted by trawlers and push-netters. After the reef deployment, they were able to fish the schools much longer and catch, as well as catch rate, increased.

The Thailand example illustrates an application of artificial habitat that likely resulted in a reduction in fishing mortality, because the increase in catches by the village fishermen was probably less than the catches previously taken by the more efficient trawlers and push-netters. This example also shows that artificial habitat can result in a change in the types of fishing gear used. Such a change may impact the species caught, catchability, and fishing mortality. Since the species composition of the catches at the artificial habitat may differ from that at the natural habitat, fishing mortality may increase for some species but decrease for others as effort shifts from natural to artificial habitat.

B. Impacts Due to Increased Exploitable Biomass but Not to Total Stock Size

Aggregation may not only cause a resource to be redistributed but may also increase the biomass of a resource exploited by a fishery. (See Fig. 5.5 part C.) If artificial habitat aggregates juveniles, thereby making them more accessible to capture, the exploitable biomass may increase as the size of the fish at entry to the fishery decreases. Conversely, aggregation may make available to fishing gear a portion of the resource that has been distributed at a low density and has not been previously exploited. An extreme case would be a resource that has not been fished because it is widely distributed at a low density at a natural habitat. Artificial habitat will aggregate the resource at a density sufficient to support a fishery, and the resource can then be exploited. From a fisherman's perspective, if a resource is not overexploited, it does not matter whether exploitable biomass is increased by aggregating unexploited biomass to artificial habitat or from new production that increases stock size. In both cases, increased catches will be achieved without increased effort.

The impact of FADs on tuna in the Philippines appears to represent this type of aggregation. There, devices known as payaos (Fig. 5.2), together with purse seines or ring nets, were introduced to the tuna fishery in the early 1970s. As a result, skipjack tuna (*Katsuwonus pelamis*) catches rose from less than 10,000 t in 1970 to 266,211 t in 1986, representing 20% of the national marine catch (Aprieto, 1988). Over 90% of the tuna caught at the FADs were less than one year old, and they were about one-half the length of a mature tuna (Aprieto, 1988). There was some concern that the heavy fishing mortality with small length at entry may result in growth overfishing (i.e., lower catches than could be achieved with larger length at entry or lower fish mortality) and recruitment overfishing (i.e., a decline in recruitment to the fishery) (Aprieto, 1988).

The question of whether FADs can cause growth overfishing has been examined by Floyd and Pauly (1984). Four factors are necessary for growth overfishing: (1) presence of small fish on the fishing ground; (2) use of gear capable of catching small fish; (3) a market for small fish; and (4) high exploitation rates. All four of these factors are present in the tuna fishery in the Philippines. Using an exploitation rate of 0.7–0.8 for skipjack tuna and yellowfin tuna (*Thunnus albacares*) with the Beverton and Holt (1966) yield equation, the yield per recruit declines by an estimated 50% when the size at entry drops from one-half to one-fourth the asymptotic length (Floyd and Pauly, 1984). The recent decline in landings from this fishery may be partly due to growth overfishing (Floyd and Pauly, 1984). Further, analysis of stomach contents suggests that the predation on juvenile tunas by adult tunas is greater at FADs than in schools in the open ocean, suggesting that FADs can increase natural mortality as well (Aprieto, 1988).

The biological impacts of this type of aggregation include all of the impacts associated with aggregation that simply redistributes exploitable biomass. However, when aggregation increases the exploitable biomass, other impacts depend on the dynamics between aggregated and unaggregated fish. Clark and Mangel (1979) developed a model for tuna purse seining in which tunas move from subsurface populations to surface schools that are fished. Applying this model to the tuna fishery with FADs shows that the potential impact of FADs on the stock depends primarily on whether the rate of movement from the unaggregated population to the FADs, as well as the mortality of the unaggregated population, exceeds the intrinsic rate of population increase (Samples and Sproul, 1985). If the rate that tunas aggregate at FADs plus non-FAD mortality exceeds the population growth rate, then high fishing mortality at the FADs alone can drive the fishable population to zero. The relationship between catches at a FAD and effort follows the typical dome-shaped production curve. The biological impact is that excessive fishing effort at FADs can result in recruitment overfishing. However, when the growth of the population exceeds the non-FAD mortality and the rate of aggregation to the FADs, no amount of fishing at the FADs can exhaust the total population (Samples and Sproul, 1985). In this case, catch increases with effort to an asymptotic value, and the biological impact is that increasing fishing effort on aggregations cannot increase the fishing mortality beyond a certain level. While the Clark and Mangel (1979) model has been applied specifically to the tuna fishery at FADs, the results also apply to demersal resources aggregated at artificial reefs.

C. Impacts Due to Increased Total Stock Size

In theory, providing additional habitat could increase the population size for some habitat-limited stocks (Fig. 5.5 part D). For example, the habitat provided by artificial reefs might result in substrata for additional food, shelter from predation, settlement habitat, and lower densities at natural reefs (Bohnsack, 1989). However, despite the large number of studies on artificial reefs, very little direct evidence indicates that artificial reefs can increase the population size of a fish stock (Bohnsack, 1989).

One unplanned experiment in the United States that may merit further study is the biological impact from the oceanic petroleum platforms off Louisiana. A single petroleum platform in a depth of 40–60 m can provide about 1 ha of hard substrate, and platforms are estimated to represent over 90% of all hard-bottom substrate off Louisiana (Scarborough-Bull, 1989). The ecosystems at these structures differ from the naturally occurring soft-bottom ecosystem and demonstrate that artificial reefs can result in the establishment of hard-substrate ecosystems, even when isolated from similar ecosystems (Scarborough-Bull, 1989). Since these platforms represent large-scale habitat alteration with apparent impacts on species composition and abundance, plus fishing areas and species targeted, a quantification of these impacts would greatly add to our understanding of the impacts of artificial habitats.

In Japan, a relatively large-scale application of artificial reefs provides some evidence that artificial reefs can increase the total stock. A significant increase in landings and catch rates of *Octopus dofleini* was observed in a small bay near Shimamaki, Hokkaido, Japan after almost 50,000 m^3 of artificial reefs were deployed (Polovina and Sakai, 1989). Additionally, availability of data from two adjacent regions in the same bay made it possible to compare relative changes in catches and catch rates as a function of artificial reef volume in each bay. While changes in environment or fishery economics could alter catches and catch rates in each region, the relative catches and catch rates should be unaltered by these factors and reflect only the impacts due to the artificial reefs.

The magnitude of the increase in octopus catches attributed to the artificial reefs was about 90 t or about 1.8 kg/m^3 of artificial reef per year. Polovina and Sakai (1989) concluded that the artificial reefs increased the exploitable biomass of octopus. This increase may have come from either an aggregation of octopus from habitat not previously exploited or from new biomass due to the additional habitat.

Unfortunately, no surveys of octopus abundance and their size structure (over the natural habitat and artificial reefs before and after the deployment) were conducted to complement the fishery data and determine whether the reefs were aggregating the octopus or actually increasing the population size. However, Polovina and Sakai (1989) addressed this issue by examining the change in catches in the two adjacent regions. They hypothesized that, if artificial reefs aggregated octopus from the entire bay, then as the octopus moved to the region with the large reef volume, an increase in catches in the region with the large volume of artificial reefs would be accompanied by a corresponding decline in catches in the adjacent region with the low volume of artificial reefs. But if the artificial reefs increased the population of octopus, changes in catches in each region would be independent of the artificial reef volume in the adjacent region and depend only on the volume within each region. The catch and effort data indicated that the catches in each region were independent of the artificial reef volume in the adjacent regions, consistent with the hypothesis that the artificial reefs did indeed increase the population of octopus (Polovina and Sakai, 1989).

Studies on the ecology of *O. dofleini* have found that the animals are almost always associated with dens, with one animal per den. So in areas without a sufficient number of dens, habitat could be limited (Hartwick *et al.*, 1978).

When the exploitable biomass in a region is heavily fished, the density of the resource above the size at entry to the fishery is very low relative to the preexploitation density. Thus, habitat is not likely to limit the population above the size at entry to the fishery, and artificial reefs that provide more habitat for this portion of the population are not likely to increase new production.

If artificial reefs are to increase new production of this resource, they might provide habitat to improve larval settlement, juvenile growth, and a reduction in juvenile natural mortality. Thus, biological impacts of artificial reefs that increase total stock size are likely to include one or more of the following: an increase in postlarval settlement, juvenile growth, and juvenile survival. However, just as with the impacts from aggregation, an increase in fishing effort, and hence, fishing mortality may also occur as the fishery responds to more accessible habitat and higher catches.

1. Estimation of Biomass Increase

In the absence of studies that quantify an increase in stock size due to artificial reefs, two simple approaches—one based on yield from natural habitat and the other based on the standing stock estimates at artificial reefs, together with an estimate of yield to biomass—can provide useful estimates of the maximum potential enhancement due to artificial reefs.

For the first approach, yield per area of artificial reefs is simply estimated from fishery yield per area of corresponding natural habitat; the resulting figure is adjusted upwards for the observed higher catches between artificial reefs and natural habitat. For example, to estimate potential fishery catches from artificial reefs in the tropics, the range of fishery production from coral reefs must first be considered. Annual fishery production per area of coral reef habitat ranges from <1 t/km^2 to 18 t/km^2, with values clustering around 5 t/km^2 (Marten and Polovina, 1982). Biomass on artificial reefs in several tropical and subtropical studies is, on average, seven times greater than on natural habitat (Stone *et al.*, 1979). If, for example, artificial reefs can support 10 times the exploitable biomass of natural coral reefs, then an average annual value for the fishery catches from an artificial reef in the tropics is 50 t/km^2 or 10 times those from a coral reef. This value is equivalent to a yield of 0.05 kg/m^2. If, as an upper bound, this yield is assumed to come from only 1 m of vertical relief, then the yield per artificial reef volume is 0.05 kg/m^3.

The second approach to estimating the new production of an artificial habitat uses the biomass estimated from local artificial reefs and then estimates the potential fishery yield as a fraction of that biomass. The Beverton and Holt (1966) yield equation can be used to determine the fraction of the biomass at the reefs that can be harvested on a sustainable basis, if estimates of a number of population parameters are available (Beddington and Cooke, 1983). However, in the absence of estimates of population parameters, an upper bound for sustainable catch can be taken as one-half the product of natural mortality and unexploited exploitable biomass ($0.5 \cdot M \cdot B_0$), where M is the natural mortality and B_0 is the unexploited exploitable biomass (Beddington and Cooke, 1983).

For example, the range of biomass estimates observed for tropical and subtropical artificial reefs is 26–698 g/m^2 (Stone *et al.*, 1979). More recently, a value of 1266 g/m^2 was documented (Brock and Norris, 1989). Taking an average value for this range of 650 g/m^2 as an average estimate of the unexploited exploitable biomass, the fishery catches can be estimated by multiplying this value by an estimate of $0.5 \cdot M$. For a tropical, fast-growing, short-lived species, M equaling 0.7 might be appropriate. A biomass of 650 g/m^2 at the artificial reefs would then support a maximum annual fishery production of about 35% of the unexploited exploitable biomass, or 228 g/m^2. Again, if yield per square meter is assumed to be due to just 1 m of vertical relief, then in this example, 0.2 kg/m^3 is the upper bound for the potential fishery yield from artificial reefs.

Once an estimate of the fishery production due to new production from the artificial reefs is available for a specific application, this estimate can be compared with the actual catches from the reefs to determine to what extent they are functioning as fish aggregators. Total catches at artificial reefs have been documented at 8 kg/m^3 of artificial reef from the Philippines and 5–20 kg/m^3 from Japan (Sato, 1985; Bojos and Van de Vusse, 1988). Of course these catches include fishes aggregrated by the reefs as well as any new production due to the reefs. If the range of catches of 5–20 kg/m^3 of artificial reef represents a range for tropical applications, then based on the example previously considered, estimates of new production due to artificial reefs are on the order 0.05–0.2 kg/m^3, indicating that the catches are primarily fishes aggregated by the reefs and greatly exceed the maximum that could be expected from new production.

This discussion is primarily meant to illustrate two approaches that can be used to estimate the relative magnitude of new and aggregated production attributable to artificial habitats, in order to determine how the structures are functioning and their role in fishery management. Each application needs to be evaluated based on the biological and fishery information specific to that application. For example, the growth of oysters and mussels on reefs in eutrophic waters may result in substantial new shellfish production (Fabi *et al.*, 1989). Chapter 3 presents a discussion on the potential of artificial habitats to provide new production as a function of the ecological characteristics of species at the habitat. Also see Chapter 3 for more comparisons of catches and biomasses between natural and artificial reefs.

III. Discussion

Artificial habitats clearly play a role in fishing systems worldwide, and are increasingly employed by fishery and environmental managers in natural resources conservation and planning. Aspects of that role for artisanal fisheries, and fisheries in general, are presented in the following section.

A. Artisanal Fishing

Artificial habitats have proven particularly effective for artisanal applications where fishing effort is relatively low. However, since such structures serve to change the distribution of fishing effort and fishes, they must be viewed within an overall fishery management plan. Their impacts should be considered in a broad socioeconomic context, rather than just in biological terms or changes in CPUE.

Artificial habitats can substantially reduce travel and search time for artisanal fishermen and improve the catchability of their gear. As long as the total fishing effort in the resource is not great enough to result in overfishing, the effects of these structures on the resource are beneficial. Gear competition between fishermen at the artificial reefs and FADs is a potential problem if effort is not regulated, but these structures could also serve to redistribute fishing effort to resolve competition.

Artificial habitats may be useful in closing areas to trawling, to protect juveniles in shallow nursery grounds, and to provide fishing sites for artisanal fishermen using gear that captures mature fish. The deployment of artificial reefs and FADs ideally should be a community project and fishermen should be involved in their planning, construction, and maintenance.

Artificial reefs and FADs built with local materials of opportunity have a certain appeal, but care should be taken to avoid depleting local forests and mangroves, or polluting the environment with inappropriate materials. Longer lasting structures built from properly ballasted scrap tires and concrete may ultimately prove more economical.

B. Fisheries Management and Other Applications

In the presence of heavy fishing effort, artificial reefs and FADs alone may not be economically beneficial. Measures that regulate gear and the fishing effort at artificial reefs and FADs may be required to avoid resource overfishing, user conflicts, and to improve fishery economics. While the literature documents many studies on the ecology at artificial structures, studies on the broader fishery management and socioeconomic impacts of these structures are lacking (see Chapter 7). For progress to be made in understanding the applications of artificial reefs and FADs, scientists and managers must deploy these structures within an overall fishery management plan consistent with the limitations of the particular artificial habitat. Finally, it is useful to view the application of artificial habitats as a decision to allocate space (the site of the habitat) and marine resources to certain user groups. This allocation and the impacts on all user groups should be understood and consistent with the objective of the artificial habitat.

The following list gives some examples of potential applications of artificial habitats that address specific management needs and that take advantage of the way artificial habitats can change the distribution of resources and fishermen, alter gear, and influence size and species harvested.

- When fishery managers wish to reduce fishing effort, artificial habitats may serve as a "bargaining chip" in negotiation. Artificial habitats can create fishing grounds close to port. Such proximity can improve the economics of fishermen by reducing expenses and increasing catchability, perhaps making it easier for fishermen to accept reductions in overall catch.
- When heavy trawling of near-shore nursery areas results in high mortality of juveniles, artificial reefs can be used to close an area to trawlers by creating unsuitable conditions for trawling.

- When one resource is overexploited, artificial habitats can serve to shift fishing effort to another resource. If soft-bottom resources are heavily fished, artificial habitats may be used to shift some fishing effort to coastal pelagic or hard-bottom resources.
- When competition between resource users is a problem, artificial habitats can be used to separate them. In cases of competition between artisanal fishermen and trawlers, artificial reefs can be used to create areas unsuitable for trawling, but suitable for artisanal usage. Sport divers might avoid competition with other types of fishermen for sites by identifying an area unused for fishing, regulating a prohibition of fishing at the site, and then deploying artificial reefs there to create a desirable dive site.

From a biological perspective, artificial habitat may function in one or all of the following ways: (1) to redistribute exploitable biomass, (2) increase exploitable biomass by aggregating previously unexploited biomass, and (3) improve aspects of survival and growth, thereby providing new production. In all three functions, artificial habitats have the potential to alter fishing effort, gear, size of fish at entry to the fishery, species targeted, and catch. The impact of change in fishing mortality on the stock depends on the relative level of exploitation and the rate of movement of the resource to the artificial habitat.

In artificial reef applications, it is possible to estimate the maximum catches from new exploitable biomass due to the artificial reef, and compare this with the actual catches to determine the extent to which the artificial reef is serving as a benthic aggregating device.

More rigorous experimental designs are needed to document the biological impacts of artificial habitat. These designs need to use large numbers of habitat structures to ensure that sufficient statistical power exists to detect impacts in the presence of considerable natural variation typical of many ecosystems. Also, they may require a control site without artificial habitat. Data of a time series should be collected at the treatment and control sites before and after the deployment of the artificial habitat. Fishery-dependent and fishery-independent data should be collected on an appropriate spatial scale and resolution to detect impacts at the artificial and natural habitats. (See Chapter 6.)

Since artificial habitat changes the spatial distribution and density of resources and the fishing effort, standard fishery models, which do not explicitly treat this spatial dimension adequately, may not represent the data fairly. For example, application of the Clark and Mangel (1979) model has proven highly useful for understanding processes at FADs. Further application of this model, along with habitat and diffusion models, should result in more realistic models to evaluate potential impacts of artificial habitat (Mullen, 1989; MacCall, 1990).

References

Ambrose, R. F. 1990. Technical report to the California coastal commission. Section H. Mitigation. Report of the Marine Review Committee, Inc., Santa Barbara, California.

Andree, S., editor. 1988. Florida artificial reef summit. Report 93. Florida Sea Grant College, Gainesville.

Aprieto, V. L. 1988. Aspects of management of artificial habitats for fisheries: The Philippine situation. Pp. 102–110 *in* Report of the Workshop on Artificial Reefs Development and Management, ASEAN/SF/88/GEN/8. September 13–18, 1988. Penang, Malaysia.

Beddington, J. R., and J. G. Cooke. 1983. The potential yield of fish stocks. FAO Fisheries Technical Paper 242. United Nations Food and Agricultural Organization, Rome.

Beverton, R. J. H., and S. J. Holt. 1966. Manual of methods for fish stock assessment. Part II. Tables of yield functions. FAO Fisheries Technical Paper 38. United Nations Food and Agricultural Organization, Rome.

Bohnsack, J. A. 1989. Are high densities of fishes at artificial reefs the result of habitat limitation or behavioral preference? Bulletin of Marine Science 44:631–645.

Bohnsack, J. A., and D. L. Sutherland. 1985. Artificial reef research with recommendations for future priorities. Bulletin of Marine Science 37:11–39.

Bojos, R. M., and F. J. Vande Vusse. 1988. Artificial reefs in Philippine artisanal fishery rehabilitation. Pp. 162–169 *in* Report of the Workshop on Artificial Reefs Development and Management, ASEAN/SF/88/GEN/8. Penang, Malaysia.

Bombace, G. 1989. Artificial reefs in the Mediterranean Sea. Bulletin of Marine Science 44: 1023–1032.

Brock, R. E., and J. E. Norris. 1989. An analysis of the efficacy of four artificial reef designs in tropical waters. Bulletin of Marine Science 44:934–941.

Buckley, R. M., D. G. Itano, and T. W. Buckley. 1989. Fish aggregation device (FAD) enhancement of offshore fisheries in American Samoa. Bulletin of Marine Science 44:942–949.

Campos, J. A., and C. Gamboa. 1989. An artificial tire-reef in a tropical marine system: A management tool. Bulletin of Marine Science 44:757–766.

Chang, K.-H. 1985. Review of artificial reefs in Taiwan: Emphasizing site selection and effectiveness. Bulletin of Marine Science 37:143–150.

Clark, C. W., and M. Mangel. 1979. Aggregation and fishery dynamics: A theoretical study of schooling and the purse seine tuna fisheries. Fishery Bulletin 77:317–337.

D'Itri, F. M., editor. 1985. Artificial reefs: Marine and freshwater applications. Lewis Publishers, Inc., Chelsea, Michigan.

Fabi, G., L. Fiorentini, and S. Giannini. 1989. Experimental shellfish culture on an artificial reef in the Adriatic Sea. Bull. Mar. Sci. 44, 923–933.

Feigenbaum, D., A. Friedlander, and M. Bushing. 1989. Determination of the feasibility of fish attracting devices for enhancing fisheries in Puerto Rico. Bulletin of Marine Science 44:950–959.

Floyd, J. M., and D. Pauly. 1984. Smaller size tuna around the Philippines—can fish aggregating devices be blamed? FAO INFOFISH Marketing Digest 5:25–27.

Grove, R. S., C. J. Sonu, and M. Nakamura. 1989. Recent Japanese trends in fishing reef design and planning. Bulletin of Marine Science 44:984–996.

Hartwick, E. B., P. A. Breen, and L. Tulloch. 1978. A removal experiment with *Octopus dofleini* (Wulker). Journal of the Fisheries Research Board of Canada 35:1492–1495.

Haughton, M. O., and K. A. Aiken. 1989. Biological notes on artificial reefs in Jamaican waters. Bulletin of Marine Science 44:1033–1037.

Hueckel, G. J., R. M. Buckley, and B. L. Benson. 1989. Mitigating rocky habitat loss using artificial reefs. Bulletin of Marine Science 44:913–922.

Hung, E. W. F. 1988. Artificial reefs development and management in Malaysia. Pp. 27–51 *in* Report of the Workshop on Artificial Reefs Development and Management. ASEAN/SF/88/GEN/8. Penang, Malaysia.

Kakimoto, H. 1984. Ecological study of the Bastard halibut or hirame (*Paralichthus olivaceus*) in the sea referring to the moving of adult fish. Pp. 183–189 *in* Fisheries in Japan: Flatfish. Japan Marine Products Photo Materials Association, Tokyo.

MacCall, A. D. 1990. Geographical population dynamics, harvesting and environmental management. U.S. National Marine Fisheries Service, Southwest Fisheries Center, Tiburon, California.

Marten, G. G., and J. J. Polovina. 1982. A comparative study of fish yields from various tropical ecosystems. Pp. 255–289 *in* D. Pauly and G. I. Murphy, editors. Theory and management of tropical fisheries. Proceedings of the ICLARM Conference 9, January 12–21, 1981. Cronulla, Australia.

McGurrin, J. M., R. B. Stone, and R. J. Sousa. 1989. Profiling United States artificial reef development. Bulletin of Marine Science 44:1004–1013.

Miclat, R. I. 1988. Artificial reef development—the Philippine experience. Pp. 63–86 *in* Report of the Workshop on Artificial Reefs Development and Management. ASEAN/SF/88/GEN/8. Penang, Malaysia.

Milon, J. W. 1989. Artificial marine habitat characteristics and participation behavior by sport anglers and divers. Bulletin of Marine Science 44:853–862.

Mullen, A. J. 1989. Aggregation of fish through variable diffusivity. Fishery Bulletin 87:353–362.

Myatt, E. N., and D. O. Myatt, III. 1990. A study to determine the feasibility of building artificial reefs in Maryland's Chesapeake Bay. Maryland Department of Natural Resources, Tidewater Administration, Fisheries Division, Annapolis.

Polovina, J. J., and I. Sakai. 1989. Impacts of artificial reefs on fishery production in Shimamaki, Japan. Bulletin of Marine Science 44:997–1003.

Prince, E. D., O. E. Maughan, and P. Brouha. 1985. Summary and update of the Smith Mountain Lake artificial reef project. Pp. 401–430 *in* F. M. D'Itri, editor. Artificial reefs: Marine and freshwater applications. Lewis Publishers, Inc., Chelsea, Michigan.

Reggio, V. C., Jr., compiler. 1989. Petroleum structures as artificial reefs: A compendium. Proceedings of the Fourth International Conference on Artificial Habitats for Fisheries, Rigs-to-Reefs Special Session, November 4, 1987, Miami, Florida. OCS Study/MMS 89-0021. U.S. Minerals Management Service, New Orleans, Louisiana.

Samples, K. C. 1989. Assessing recreational and commercial conflicts over artificial fishery habitat use: Theory and practice. Bulletin of Marine Science 44:844–852.

Samples, K. C., and J. T. Sproul. 1985. Fish aggregating devices and open-access commercial fisheries: A theoretical inquiry. Bulletin of Marine Science 37:305–317.

Sato, O. 1985. Scientific rationales for fishing reef design. Bulletin of Marine Science 37:329–335.

Scarborough-Bull, A. 1989. Some comparisons between communities beneath petroleum platforms off California and in the Gulf of Mexico. Pp. 47–50 *in* V. C. Reggio, Jr., compiler. Petroleum structures as artificial reefs: A compendium. Proceedings of the Fourth International Conference on Artificial Habitats for Fisheries, Rigs-to-Reefs Special Session, November 4, 1987, Miami, Florida, OCS Study/MMS 89-0021. U.S. Minerals Management Service, New Orleans, Louisiana.

Sinanuwong, K. 1988. Artificial reefs construction in Nakornsrithammarat Province. Pp. 130–134 *in* Report of the Workshop on Artificial Reefs Development and Management. ASEAN/SF/88/GEN/8. Penang, Malaysia.

Stanley, D. R, and C. A. Wilson. 1989. Utilization of offshore platforms by recreational fishermen and scuba divers off the Louisiana coast. Pp. 11–24 *in* V. C. Reggio, Jr., compiler. Petroleum structures as artificial reefs: A compendium. Proceedings of the Fourth International Conference on Artificial Habitats for Fisheries, Rigs-to-Reefs Special Session, November 4, 1987, Miami, Florida, OCS Study/MMS 89-0021. U.S. Minerals Management Service, New Orleans, Louisiana.

Stone, R. B., H. L. Pratt, R. O. Parker, Jr., and G. E. Davis. 1979. A comparison of fish populations on an artificial and natural reef in the Florida Keys. Marine Fisheries Review 41(9):1–11.

Sungthong, S. 1988. Artificial reefs development as a tool for fisheries management in Thailand. Pp. 87–91 *in* Report of the Workshop on Artifijcial Reefs Development and Management, ASEAN/SF/88/GEN/8. Penang, Malaysia.

U.S. National Research Council. 1988. Fisheries technologies for developing countries. Report of an ad hoc panel of the Board on Science and Technology for International Development. National Academy Press, Washington, D.C.

Yamane, T. 1989. Status and future plans of artificial reef projects in Japan. Bulletin of Marine Science 44:1038–1040.

Young, C. 1988. Major artificial reef in WA follows SA lead. Australian Fisheries 47(12):26–28.

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SEASONAL ABUNDANCE, HABITAT USE, AND DIET OF SHOREBIRDS IN ELKHORN SLOUGH, CALIFORNIA

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Large numbers of migrant and resident shorebirds feed and roost along the open coast, bays, sloughs, and marshes of California. However, more than 70% of coastal wetlands in California have been degraded by diking, filling, pollution, and other human activities (Speth 1979). Elkhorn Slough is one of the largest remaining salt marshes in California available to migratory shorebirds using the Pacific Flyway. Identification and conservation of critical habitats are required for an understanding of shorebird ecology and effective management of our resources (Senner and Howe 1984). Habitat use and foraging behavior vary from site to site (Baker and Baker 1973, Connors et al. 1979, Page et al. 1979), determined partially by the seasonal concurrence of shorebird movements and reproductive status, and habitat availability and preference. Abiotic factors (e.g., wind, tide, and temperature), as well as bird size and morphology, also influence distribution and behavior of shorebirds (Burger et al. 1977, Burger 1984).

Although some general patterns of shorebird distribution along the California coast are well documented (Jurek 1974, Shuford et al. 1989), trends in shorebirds' seasonal abundance and use of Elkhorn Slough wetlands are relatively unknown. Browning (1972) listed species, months of peak abundance, and maximum numbers of shorebirds in the slough. Seasonal occurrence and relative abundance of shorebirds in Elkhorn Slough were included in a broad census of California's wetland system, although observations were spatially and temporally limited (Jurek 1974).

Our objectives in this study were to describe the seasonal patterns in species composition and abundance of shorebirds in Elkhorn Slough, and to identify components of the ecosystem that support this assemblage. Use of habitat (intertidal mudflats, salt pond, and salt marsh) and feeding ecology of selected species were assessed.

Since 1983, more than 130 ha of diked wetlands have been returned to tidal action on the Elkhorn Slough National Estuarine Research Reserve. The salt ponds adjacent to the slough were exposed to tidal action in 1984. The present study, therefore, provides baseline information necessary for long-term monitoring of shorebirds in these newly restored marsh habitats.

STUDY AREA AND METHODS

Elkhorn Slough is a shallow tidal embayment and seasonal estuary on Monterey Bay (Figure 1), located about 160 km south of San Francisco, California. The slough has an axial length of 10 km and maximum width of 100 m at its mouth. The main channel is bordered by mudflats and is intersected by several small tidal creeks. Grain size of intertidal sediment decreases progressively from the mouth (82% sand particles >64 µm; 18% silt) to the most inland areas of the slough (67% clay and 33% silt; C. Jong, Univ. California, Santa Cruz, unpubl. data). During this study, water depth in the main channel below mean lower low water (MLLW) was 5 m at the

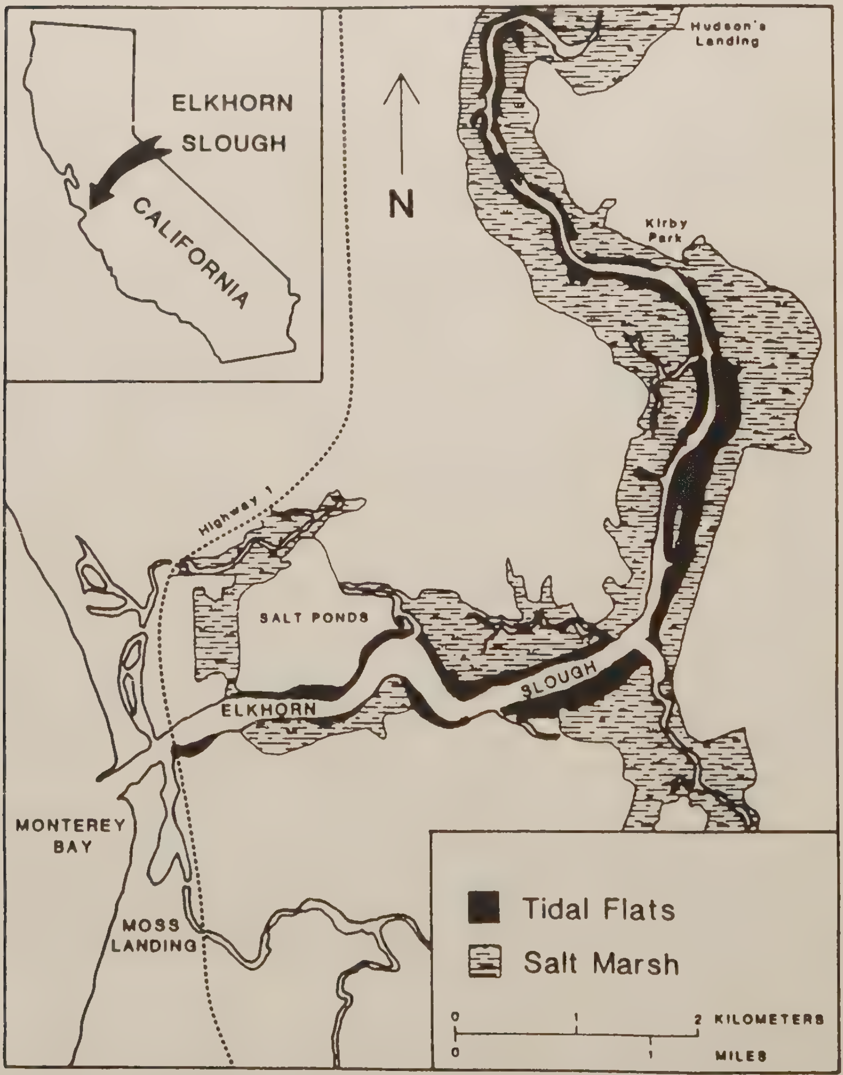

ELKHORN
SLOUGH
CALIFORNIA
N
Hudson's Landing
Kirby Park
Highway 1
SALT PONDS
ELKHORN
SLOUGH
MONTEREY BAY
MOSS LANDING
■ Tidal Flats
▤ Salt Marsh
0
1
2 KILOMETERS
0
1
MILES

Figure 1. Shorebird survey area of Elkhorn Slough, indicating intertidal mudflats, salt marsh, and salt ponds.

mouth and <1 m at the most inland station; the mean tidal range was 1.1 m (Smith 1973, Broenkow 1977). About 170 ha of intertidal mudflats are exposed at MLLW (Browning 1972). Diked evaporating salt ponds (77 ha) are adjacent to Elkhorn Slough (Figure 1). An extensive salt marsh (583 ha) is located primarily on the northwest edge of the slough, and pickleweed (*Salicornia virginica*) is the dominant plant cover.

Surveys

We conducted our most intensive shorebird surveys from 1 November 1977 to 27 February 1980, along the main channel of Elkhorn Slough from California State Highway 1 to Hudson's Landing (Figure 1). At low tide, shorebirds on each intertidal mudflat and in adjacent salt marsh were identified and counted by one to four observers. Surveys were conducted from a small boat and lasted 1–4 hours. The direction of the survey route along the main channel and the state of the tides varied during each survey. All surveys were conducted between +1.2 and –0.1 m, relative to MLLW; mudflats were exposed within this range but the extent of exposure varied; see Ramer (1985) for tidal conditions during each survey. To minimize error associated with movement of birds among areas, we excluded any large flocks that likely were counted earlier. Number of shorebirds was converted to biomass by multiplying by the average weight of each species (Page et al. 1979) . Because of limited time at low tide, not all species were counted during every survey; abundance of common species, however, was determined at least once a month. Number of surveys during the year, therefore, is different for each species. Only surveys that included counts of all common species were used to estimate total and seasonal abundance of shorebirds.

To assess temporal patterns in abundance of shorebirds, we defined seasons as fall (July–October), winter (November–February), and spring (March–June). Summer was identified as the period (usually June) between the lowest abundance in spring and the increase in numbers in fall.

Habitat Use

Salt Ponds. To document shorebird use of salt ponds (Figure 1), we conducted additional surveys during October and November 1978. Numbers of birds roosting and feeding at five ponds were recorded over 3 hours on each of 12 days. Observations focused on the most abundant species: Western Sandpiper (*Calidris mauri*), Least Sandpiper (*C. minutilla*), and Dunlin (*C. alpina*).

Salt Marshes. We estimated relative frequency of roosting and feeding on 9 and 26 March 1979 for 10 minutes at 1-hour intervals in each of 3 hours during high tide at seven stations throughout the marsh (Figure 1).

Diet

From November 1978 to December 1979, stomach contents of Western Sandpipers (N = 25), Willets (*Catoptrophorus semipalmatus*; N = 21), and Marbled Godwits (*Limosa fedoa*; N = 24) were collected, primarily at one mudflat along the main channel of the slough. These were the most abundant species that represented a gradient in bill length and body size. Feeding birds were shot and stomachs were injected with 10% formalin in the field. Stomach contents of seven additional Western Sandpipers were collected by means of a stomach pump after feeding birds were trapped in a net in the salt ponds. Few prey items remained in the stomachs after pumping (Ramer 1985); this effective technique should be considered in place of sacrificing birds for future diet studies. All data on diet of Western Sandpipers were combined for analysis.

Prey parts were identified to the lowest possible taxon; number and relative volume (%) of each prey category in a stomach were estimated. Prey identification frequently was based on recognizable parts only, such as bivalve hinge fragments, amphipod uropods, and polychaete setae. A minimum prey number of 1 was assigned to taxon represented solely by parts (e.g., polychaete setae or pieces of algae). Prey categories in each stomach were ranked according to their index of relative importance (IRI; Pinkas et al. 1971), a function of relative frequency of occurrence (FO), relative number (N), and relative volume (V): $\mathrm{IRI} = (N + V) \times (\mathrm{FO})$.

RESULTS

Seasonal Patterns

The most abundant shorebird species along the main channel of Elkhorn Slough were (in descending order) the Western Sandpiper, Dunlin, Least Sandpiper, dowitchers (Short-billed [*Limnodromus griseus*] and Long-billed [*L. scolopaceus*]), Marbled Godwit, American Avocet (*Recurvirostra americana*), Willet, Black-bellied Plover (*Pluvialis squatarola*), Long-billed Curlew (*Numenius americanus*), and Sanderling (*Calidris alba*). Other shorebirds occurred irregularly, and included a maximum of 46 Ruddy Turnstones (*Arenaria interpres*), 32 Semipalmated Plovers (*Charadrius semipalmatus*), 27 Whimbrels (*Numenius phaeopus*), 7 Greater Yellowlegs (*Tringa melanoleuca*), 6 Killdeers (*Charadrius vociferus*), 6 Red Knots (*Calidris canutus*), 3 Black-necked Stilts (*Himantopus mexicanus*), and 1 Lesser Yellowlegs (*Tringa flavipes*) per survey.

For the eight species common to each of 21 surveys along the main channel of Elkhorn Slough, total number increased during fall, from about 200 birds in June to 11,750 birds in November (Figure 2). From 6000 to 13,750 birds were counted during winter (the period of minimum migratory movement), and numbers decreased from spring to summer. Biomass similarly increased from 70 kg in June to 740 kg in November (Figure 2).

From counts combined by season over all years for each species, Western Sandpipers accounted for at least 75% of shorebirds present in every season (Figure 3). Numbers of each of the other species represented less than 10% of the total in any particular season. Small species (<150 grams body weight) made up at least 90% of the total number of shorebirds in all seasons (Figure 3). Total biomass was more evenly distributed between small and large (>150 grams body weight) species; one species predominated in each category. Western Sandpipers had the highest biomass of the small species, and Marbled Godwits had the highest numbers and biomass of the large species (Figure 3).

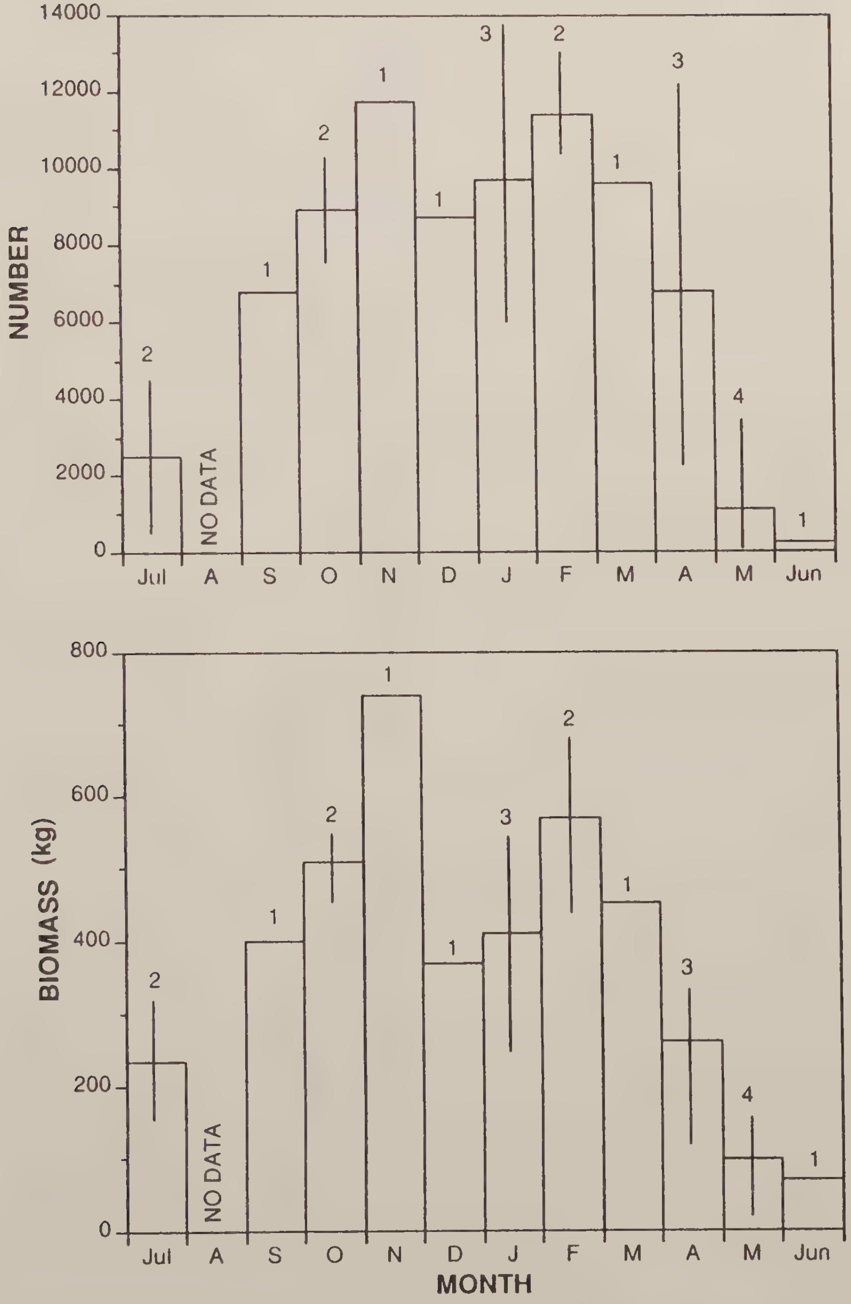
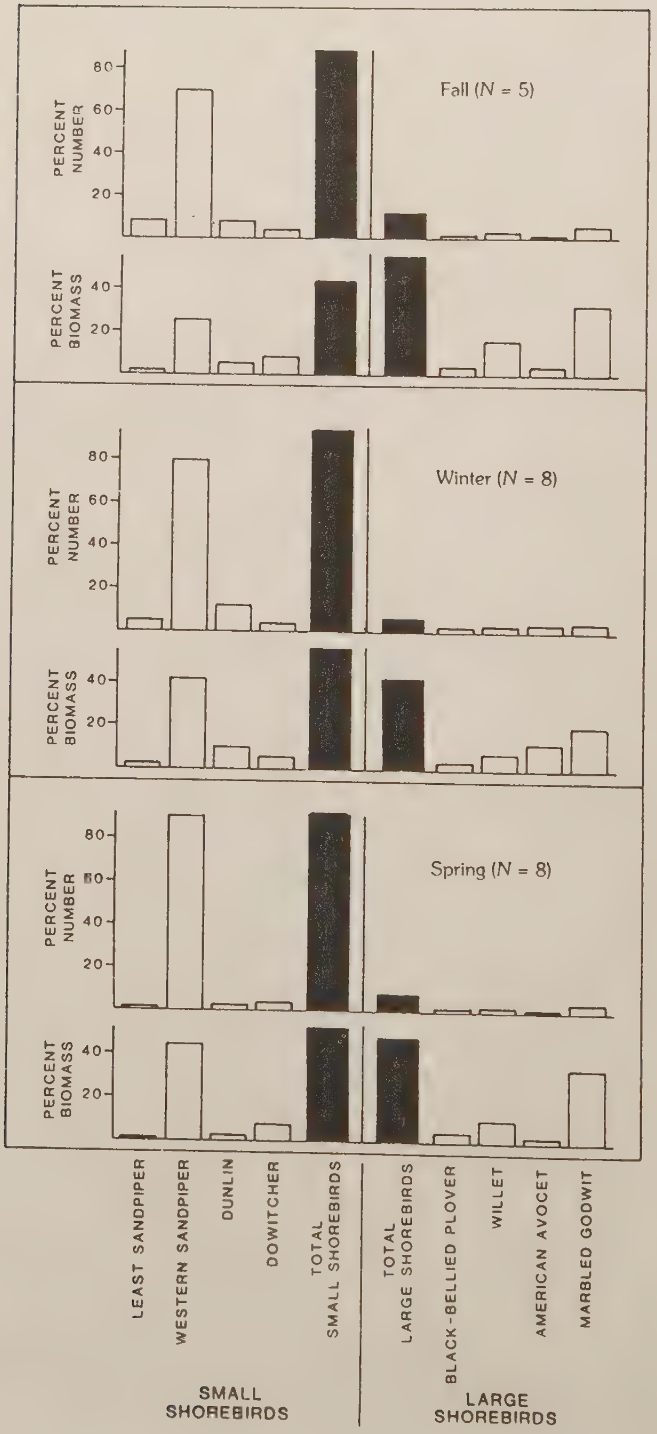


Figure 2. Seasonal changes in mean (vertical line is range) number and biomass of shorebirds along the main channel of Elkhorn Slough from November 1977 to February 1980. Number of surveys is indicated above each bar.


Fall (N = 5)
Winter (N = 8)
Spring (N = 8)
PERCENT NUMBER
PERCENT BIOMASS
80
60
40
20
LEAST SANDPIPER
WESTERN SANDPIPER
DUNLIN
DOWITCHER
TOTAL SMALL SHOREBIRDS
TOTAL LARGE SHOREBIRDS
BLACK-BELLIED PLOVER
WILLET
AMERICAN AVOCET
MARBLED GODWIT
SMALL SHOREBIRDS
LARGE SHOREBIRDS

The fall influx of most shorebirds began in June or July, except for that of Dunlins, which were not recorded until October (Figures 4 and 5). Least Sandpipers exhibited a fall peak in abundance, whereas Western Sandpipers did not (Figure 4). All common species overwintered in the slough. Numbers of Dunlins generally increased in early winter and spring. Although dowitchers were not distinguished morphologically, vocalizations indicated that more than 90% of the wintering birds were Long-billed Dowitchers. No small shorebird species were sighted in the area during summer, but nonbreeding birds of most large species were present during June (Figure 5). There was considerable variation in patterns of abundance for large and small species (Figures 4 and 5).

Habitat Use

Salt Ponds. Small shorebirds used the salt ponds primarily as a roost during high tide, secondarily as a feeding area. Western Sandpipers, Least Sandpipers, and Dunlins roosted in dense multi-species flocks in shallow ponds at the northwest corner and along dikes. From 830 to 20,730 small shorebirds (primarily Western Sandpipers and Dunlins) were counted per survey (*N* = 12) in the salt ponds. Of the small shorebird species that occurred in Elkhorn Slough, most individuals roosted in the salt ponds; no large flocks roosted elsewhere in the slough. Some small shorebirds fed intermittently near roosting flocks in the salt ponds. However, on average, 78.8% (standard error = 5.7) of Western Sandpipers and Dunlins were roosting. On falling tides, small sandpipers left salt-pond roosts and flew to exposed intertidal mudflats in the slough (*N* = 15 observations).

Large shorebirds also roosted in salt ponds. We observed as many as 350 Black-bellied Plovers and 700 American Avocets roosting in tight flocks in shallow ponds during single surveys. Willets and Marbled Godwits occasionally roosted in flocks up to 500 birds per survey, with only a few individuals feeding. Long-billed Curlews were not observed in salt ponds.

Several species fed in the salt ponds and were rarely or never observed in the main slough. We saw up to 400 Red-necked Phalaropes (*Phalaropus lobatus*), 200 Red Phalaropes (*P. fulicarius*), 150 Black-necked Stilts, 100 Snowy Plovers (*Charadrius alexandrinus*), and 30 Wilson's Phalaropes (*P. tricolor*) on single surveys. American Avocets, Black-necked Stilts, Snowy Plovers, and Killdeers bred locally in the salt ponds.

Salt Marshes. Maxima of 266 Willets, 257 Marbled Godwits, and 127 Long-billed Curlews were counted during the 3-hour surveys. These large shorebirds roosted and fed in salt marshes during high tides. Although most birds were observed flying over the marsh, an average of 24.3% (S.E. = 6.6) were roosting and 13.7% (S.E. = 4.2) were feeding. As the tide receded, most Marbled Godwits flew from the marsh to feed on intertidal mudflats. In

← Figure 3. Percent composition of most abundant small (<150 g) and large (>150 g) shorebird species by number and biomass from pooled data in fall (*N* = 5 surveys), winter (*N* = 8), and spring (*N* = 8) along the main channel of Elkhorn Slough. Species are ordered with increasing body weight from left to right.

contrast, some Willets and Long-billed Curlews continued to feed in the marsh during low tides. Some small shorebirds roosted on barren mudpans or in sparsely vegetated areas of marsh, but these scattered individuals never gathered in the large aggregations that occurred in the salt ponds. Small shorebirds never roosted in dense marsh vegetation.

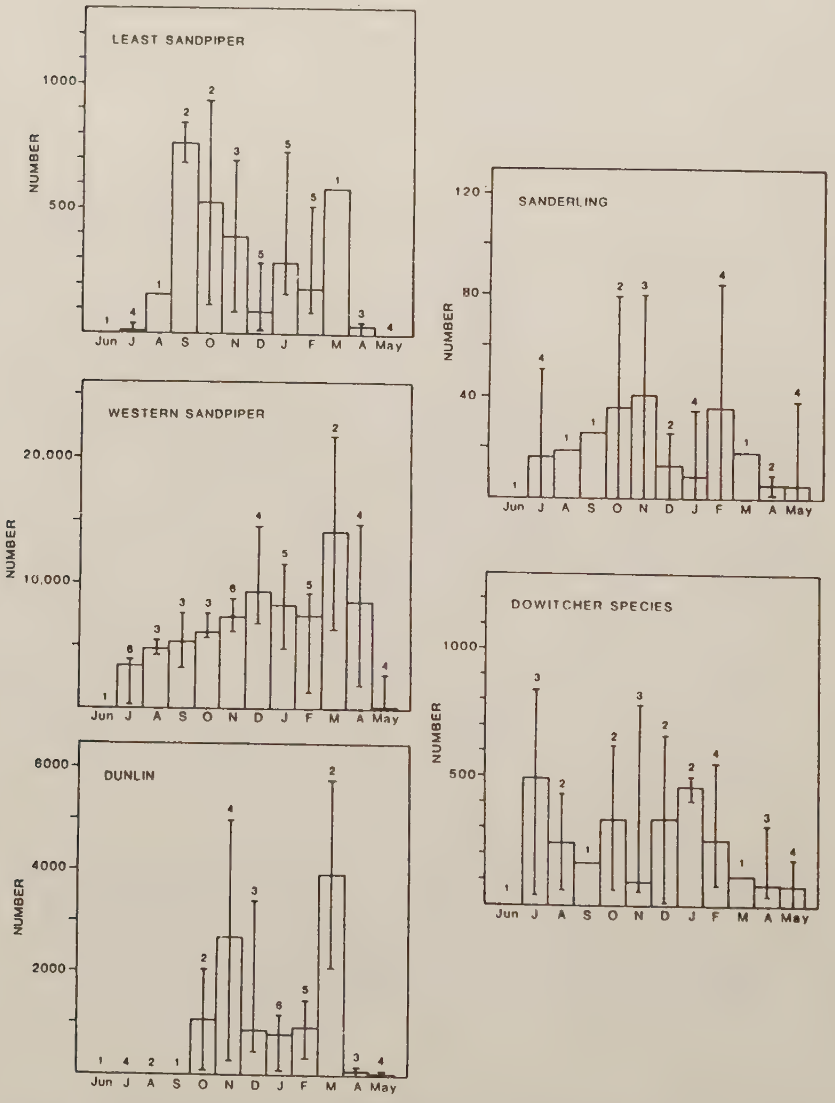


Figure 4. Median number (vertical line is range) of most abundant small (<150 g) shorebird species surveyed along the main channel of Elkhorn Slough. Number of surveys is indicated above each bar.

Mudflats. Intertidal mudflats were important feeding areas for all shorebird species. Density of Western Sandpipers that fed along the main channel of the slough increased generally with distance inland (the most muddy end of the slough), and was lowest at the most sandy intertidal flat near the mouth (Table 1). Mean densities of all large shorebird species were

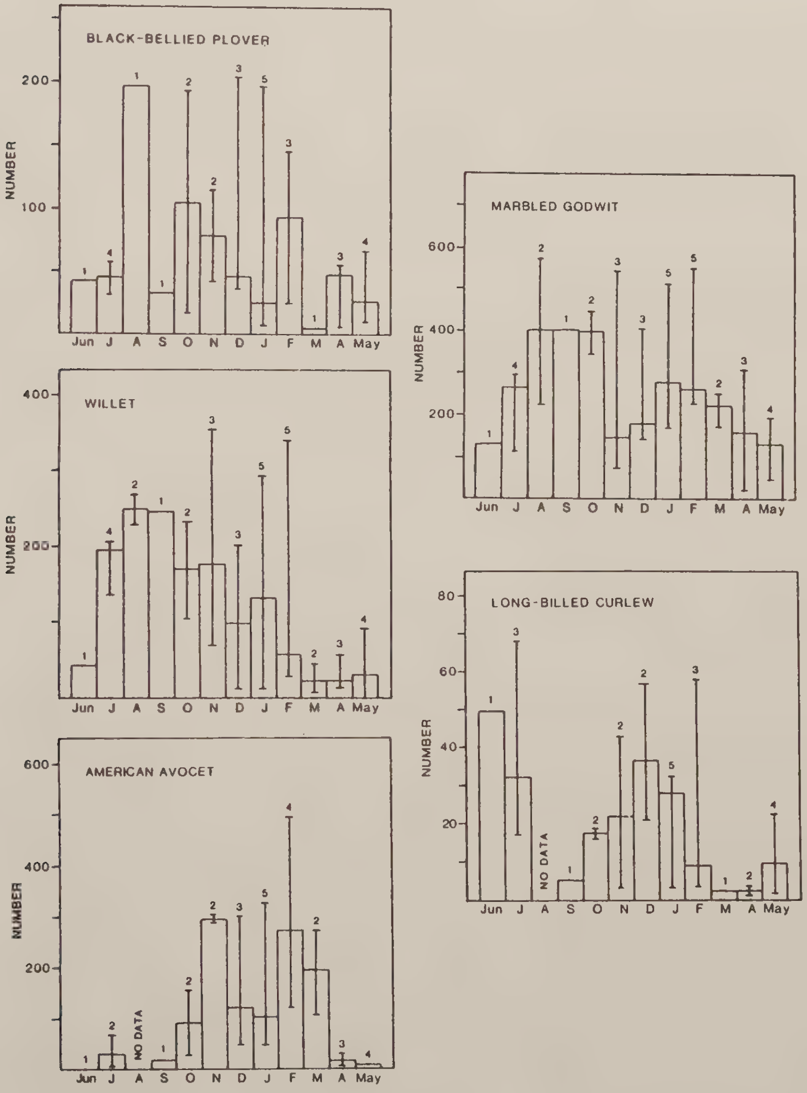


Figure 5. Median number (vertical line is range) of most abundant large (>150 g) shorebird species surveyed along the main channel of Elkhorn Slough. Number of surveys is indicated above each bar.

highest on mudflats about 3 km inland. Marbled Godwits and Sanderlings were the only species that fed in relatively high densities on the sandiest flats closest to the mouth. The relatively high mean density of Sanderlings at the most inland, muddy flat resulted from an unexpected count of 80 birds during one survey.

Diet

Western Sandpiper. Western Sandpipers primarily ate insects (mostly ephydrid fly larvae and pupae) and small infaunal invertebrates. Insect larvae and pupae ranked first in relative importance in fall and spring (Table 2). Prey composition of fall and winter samples differed markedly. Harpacticoid copepods, the bivalve *Gemma gemma*, Foraminifera, and the polychaete *Capitella capitata* occurred in at least 50% of stomachs from both seasons, but insects were not important in the winter diet (IRI = 11). Oligochaetes were found in 50% of the fall samples, but in none collected in

Table 1 Density (Number per Hectare) of Shorebirds Feeding on Intertidal Mudflats at Increasing Distance from the Mouth of Elkhorn Slough

Species	Distance up slough (km)				
	1	3	5	9	N[a]
Small Shorebirds					
Least Sandpiper	0.7[b] (0.3)	2.0 (0.7)	2.3 (0.7)	1.8 (0.6)	24
Western Sandpiper	5.5 (1.6)	51.6 (8.5)	100.6 (14.8)	64.4 (13.0)	24
Dunlin	4.4 (2.4)	7.1 (2.3)	13.2 (6.7)	10.5 (4.3)	19
Sanderling	0.7 (0.2)	0.1 (0.1)	0.1 (0.1)	0.2 (0.2)	14
Dowitcher	0.4 (0.1)	2.3 (1.0)	2.3 (0.5)	1.7 (0.5)	19
Large Shorebirds					
Black-bellied Plover	0.2 (0.0)	0.9 0.3)	0.3 (0.1)	0.1 (0.0)	23
Willet	0.4 (0.1)	1.4 (0.4)	1.2 (0.3)	0.6 (0.1)	22
American Avocet	0.3 (0.2)	2.1 (0.7)	1.0 (0.3)	0.5 (0.2)	16
Marbled Godwit	2.9 (0.6)	3.0 (0.5)	1.6 (0.3)	0.5 (0.2)	21
Long-billed Curlew	0.1 (0.0)	0.3 (0.1)	0.1 (0.0)	0.1 (0.0)	21

[a] Number of surveys.

[b] For each species, top row of figures is mean density, bottom row (in parentheses) is standard error.

winter. Amphipod crustaceans (*Corophium* spp. and Gammaridae) were the most important prey items in winter but nearly absent in fall. Although the relative occurrence of polychaetes (*Capitella capitata*) was high in fall and winter (FO = 75% and 86%, respectively), total number, volume, and IRI values probably were underestimated because of digestion (Page and Stenzel 1975, Quammen 1984). Algae, plant debris, and Foraminifera probably were ingested incidentally with other prey.

Willet. The highest-ranking prey of Willets in all seasons was the crab *Hemigrapsus oregonensis* (Table 3). In winter, another crab, *Pachygrapsus crassipes*, occurred in 63% of the stomachs, and ranked second in relative importance; crabs were the only prey in winter samples. In spring, Willets ate crabs and the opisthobranch snail *Haminoea*. Fall samples were more diverse, with eight prey categories. Willets ate many fewer species than did Western Sandpipers.

Marbled Godwit. In fall, polychaete worms (including *Capitella capitata*, *Boccardia hamata*, and Spionidae) ranked high in occurrence and relative importance (Table 4). Bivalves (*Gemma gemma* and *Macoma* spp.) also were relatively important (IRI = 942 and 412, respectively). In winter samples, these two bivalves were among the highest-ranking prey items. Polychaetes and crabs were secondarily important. No prey items occurred in more than 44% of the winter stomachs. In spring, the highest-ranked

Table 2 Seasonal Variation in the Diet of Western Sandpipers

	Fall (12)[a]		Winter (7)		Spring (11)	
Prey	%FO[b]	IRI[c]	%FO	IRI	%FO	IRI
Insect larvae	68	3063	14	11	100	15510
Seeds	68	2564	0	0	36	72
Harpacticoida	58	2115	57	237	0	0
Gemma gemma	50	801	57	157	18	119
Insect debris	42	627	43	293	0	0
Foraminifera	50	618	86	983	9	2
Capitella capitata	75	337	86	183	0	0
Algae and plant debris	67	321	57	318	54	76
Oligochaeta (Tubificidae)	50	172	0	0	0	0
Spionidae	42	119	0	0	0	0
Corophium spp.	17	7	100	5911	0	0
Gammaridae	0	0	71	3328	0	0
Ostracoda	25	23	100	1666	45	191
Crustacean fragments	25	36	43	525	0	0
Cumella vulgaris	25	23	43	317	0	0
Polychaete setae	8	1	43	179	0	0
Allorchestes angusta	0	0	43	70	9	6

[a] Number of stomachs examined in parentheses.
[b] FO, frequency of occurrence.
[c] IRI, index of relative importance (see text).

Table 3 Seasonal Variation in the Diet of Willets[a]

	Fall (5)		Winter (8)		Spring (8)	
Prey	%FO	IRI	%FO	IRI	%FO	IRI
Hemigrapsus oregonensis	40	855	88	9620	63	7201
Crab fragments	20	801	38	331	13	131
Orchestia traskiana	20	740	0	0	0	0
Hemigrapsus spp.	20	531	0	0	13	57
Eggs	20	389	0	0	0	0
Bivalvia	20	229	0	0	0	0
Algae and plant debris	20	219	0	0	13	181
Ostracoda	20	202	0	0	0	0
Pachygrapsus crassipes	0	0	63	3547	13	310
Haminoea/Bulla	0	0	0	0	13	129

[a] For abbreviations see Table 2.

prey categories were the crab *H. oregonensis* and the bivalve *Macoma* spp. Prey type, size, and diversity of the Marbled Godwit were intermediate between those of the Willet and the Western Sandpiper. Again, algae probably were eaten incidentally with other prey and occurred in the Marbled Godwit's diet throughout the year.

Table 4 Seasonal Variation in the Diet of Marbled Godwits[a]

	Fall (6)		Winter (9)		Spring (9)	
Prey	%FO	IRI	%FO	IRI	%FO	IRI
Polychaeta	83	5860	33	180	0	0
Capitella capitata	33	983	44	114	0	0
Gemma gemma	33	942	33	375	11	70
Spionidae	67	694	44	114	0	0
Macoma spp.	17	412	44	2248	44	1466
Bivalvia	17	211	33	776	22	301
Algae	50	115	33	599	67	1799
Boccardia hamata	17	95	6	0	0	0
Protothaca staminea	17	95	11	12	22	385
Macoma nasuta	0	0	44	1016	0	0
Hemigrapsus spp.	17	1	22	259	0	0
Hemigrapsus oregonensis	0	0	11	223	44	1926
Pachygrapsus crassipes	0	0	11	124	0	0
Crab fragments	17	16	0	0	22	675
Eggs	0	0	0	0	22	155

[a] For abbreviations see Table 2.

DISCUSSION

Relative to most coastal wetlands on the Pacific Flyway, Elkhorn Slough supports large numbers of wintering and migrating shorebirds, representing nearly 40 species (Point Reyes Bird Observatory [PRBO], unpubl. data). During recent surveys of 48 California wetlands that likely have more than 1000 shorebirds, Elkhorn Slough ranked third in gross number of birds, holding 1–3 % (>19,000 birds) of all shorebirds counted in spring and 5–6% (>30,000 birds) of those counted in fall (PRBO, Pacific Flyway Project, unpubl. data from September 1988 to April 1990). Comparison with Humboldt Bay, which ranked a close second in gross number of birds but which is 20–30 times larger in surface area, shows the importance of Elkhorn Slough to shorebirds along the central coast. Numbers of birds were highest (relative abundance 73-88%) in the San Francisco Bay system, whose surface area is several orders of magnitude larger than that of any other California wetland.

Shorebirds common in Elkhorn Slough occur commonly in other coastal wetlands along the California coast. As in Elkhorn Slough, either Willets or Marbled Godwits were among the most abundant large shorebirds, and Western Sandpipers, Least Sandpipers, dowitchers, and Dunlins were among the most abundant small shorebirds in San Diego Bay (Jehl and Craig 1970), San Francisco Bay (Page et al. 1990), wetlands from Point Reyes to Bodega Bay (Shuford et al. 1989), and Humboldt Bay (Gerstenberg 1979). The same large species that oversummer at Elkhorn Slough do so elsewhere along the California coast (Jurek 1974, Shuford et al. 1989).

There are some differences in abundance, however, between wetlands. Whereas Western Sandpipers clearly were the dominant species in Humboldt Bay, Elkhorn Slough, and San Francisco Bay, Least Sandpipers were as abundant in the Point Reyes area; Willets, Marbled Godwits, Least Sandpipers, and Western Sandpipers were equally abundant in Morro Bay (Stenzel et al. 1989, Page et al. 1990). Differences among wetlands in occurrence and relative abundance of shorebirds can be influenced by climate, hydrography, and habitat resources (Shuford et al. 1989).

Because species-specific density has not been estimated for shorebirds in most locations, comparisons among wetlands are difficult. Even though the most abundant wintering shorebird species were the same in Elkhorn Slough as from Point Reyes to Bodega Bay, densities in the slough usually were higher; e.g., mean densities of Western Sandpipers and American Avocets in the slough were about six times higher than maximum densities in the wetlands from Point Reyes to Bodega Bay (Table 5; Page et al. 1983).

Seasonal patterns in abundance of each shorebird species in Elkhorn Slough, as at any location, reflect time of migration and routes of travel between breeding and wintering grounds. In general, most species of wintering shorebirds move into California from July to November; spring exodus to the breeding grounds occurs from late March to early May (Jurek 1974, Shuford et al. 1989). In coastal wetlands of central California, peaks in abundance of fall migrants usually are apparent for Short-billed Dowitch-

Table 5 Mean Winter Density (Number per 100 ha) of Shorebirds on Tidal Flats in Elkhorn Slough and Range of Densities in Point Reyes–Bodega Bay Area

Species	Elkhorn Slough	Point Reyes–Bodega Area[a]
Least Sandpiper	213 (39)[b]	47–180
Western Sandpiper	6020 (490)	59–1055
Dunlin	1025 (243)	634–1299
Sanderling	23 (7)	16–129
Dowitcher (two species)	255 (63)	18–71
Black-bellied Plover	61 (14)	94–141
Willet	114 (23)	93–140
American Avocet	165 (28)	0–27
Marbled Godwit	223 (28)	113–758
Long-billed Curlew	20 (4)	0–12

[a] Includes Bolinas Lagoon, Limantour Estero, Drake's Estero, and Abbott's Lagoon. Data from Page et al. (1983).

[b] Figures in parentheses are standard errors.

ers, Least Sandpipers, Willets, Sanderlings, and sometimes Western Sandpipers and Black-bellied Plovers (Shuford et al. 1989). Marbled Godwits, Long-billed Curlews, American Avocets, and Dunlins do not exhibit these peaks. Spring peaks in abundance are described for Western Sandpipers and dowitchers. These general patterns in seasonal abundance do not apply to all the state's wetlands. For example, a well-defined peak was noted in fall for Western Sandpipers in Bolinas Lagoon, whereas very small or no peaks were obvious elsewhere around Point Reyes (Shuford et al. 1989).

The beginning of fall migration into Elkhorn Slough in July and spring movement out of the slough in late March generally follows the established migratory periods. Timing of fall migration is dependent on age and reproductive status of individual birds; e.g., generally, adults migrate earlier than do immature birds (Page et al. 1979). This extended migration can obscure peaks from site-specific surveys such as ours. Also, because dowitcher species were not distinguished in Elkhorn Slough, the larger population of wintering Long-billed Dowitchers could have masked the peaks of migrating Short-billed Dowitchers. A comprehensive survey of the regional wetlands of Monterey Bay, as well as a long-term intensive study of Elkhorn Slough, is necessary before seasonal patterns in abundance can be described adequately.

Changes in abundance also occur because of localized movements of shorebirds (Pienkowski and Evans 1984). Local movements may be synchronous with time lags between low tides at various locations, thus extending foraging time (Connors et al. 1981). Additionally, abundance can vary with daily movement of some species to feed in inland fields (Townshend 1981, Ruiz et al. 1989). Daily movements of Willets, Marbled Godwits, Black-bellied Plovers, and Sanderlings between Elkhorn Slough and adjacent beaches of the outer coast and river mouths occurred frequently during winter (J. Warriner pers. comm.). Irregular shifts in abundance of Least Sandpipers, Western Sandpipers, Dunlin, and dowitchers between the slough and the mouths of the Pajaro and Salinas rivers (5 and 8.8 km away, respectively) also are likely, because numbers of birds in these areas seem to fluctuate with habitat availability. Elkhorn Slough is the likely source of these birds because it is the closest large area of suitable habitat.

The restoration of wetlands in Elkhorn Slough resulted in increased surface area of mudflats and up to an average of 0.8 hours phase lag of high and low water relative to Monterey predicted tides (Wong 1989); these changes can influence shorebird foraging behavior and local movements. Movements of greater distance are possible, especially to San Francisco Bay, which because of its large size may serve to attract and aggregate shorebirds on the central California coast. Near Point Reyes, for example, Marbled Godwits and American Avocets move daily from foraging grounds in Bolinas Lagoon to probable nighttime roosts in San Francisco Bay (Blick 1980, Shuford et al. 1989). Snowy Plovers also move between Monterey and San Francisco bays (J. Warriner pers. comm.).

In Elkhorn Slough, shorebirds roosted in salt marshes and salt ponds during high tide, then moved to intertidal mudflats to feed at low tide. Shorebird species were not distributed evenly over tidal flats. The increased incidence of Western Sandpipers feeding at the most muddy intertidal sites in Elkhorn Slough recalls Quammen's (1982) findings that shallow-feeding shorebirds, such as Western Sandpipers, spent more time feeding and were more successful at prey capture on intertidal mudflats having little sand. She suggested that sand interferes with detection and capture of prey (small polychaetes and oligochaetes) because of similarity in size.

Seasonal changes in the diet of the Western Sandpiper and the Marbled Godwit were considerable, and probably related to spatial and temporal variation in availability of prey, although prey populations were not sampled. In other coastal wetlands, insect larvae and pupae (Order Diptera) occur in high densities near the surface of mudflats during warm fall months and are common in the diet of some species of small shorebirds, especially Western Sandpipers (Couch 1966, Page and Stenzel 1975, Stenzel et al. 1983). Other prey species of Western Sandpipers and Marbled Godwits were among the most abundant infaunal invertebrates in the mudflats of Elkhorn Slough (Nybakken and Jong 1977). Similar prey types have been reported in the diet of Western Sandpipers (Page and Stenzel 1975, Quammen 1984) and Marbled Godwits (Recher 1966, Holmberg 1975, Page and Stenzel 1975) from other coastal areas, although the relative importance of each type varied with location.

Salt marshes were used primarily by large shorebirds. Small shorebirds were not observed in areas of Elkhorn Slough where marsh vegetation was tall and dense, but they did feed and roost in sparse vegetation of the upper-slough marsh, suggesting that use of this habitat was restricted by height and density of vegetation. Willets were the only shorebirds that fed regularly in large numbers in the salt marsh. Their diet was dominated by crabs that are abundant in vertical banks of the marsh (Sliger 1982) and larger than the infaunal prey consumed by Western Sandpipers and Marbled Godwits on intertidal mudflats. Willets have similar feeding habits in other coastal wetlands (Reeder 1951, Recher 1966, Holmberg 1975, Stenzel et al. 1976).

The salt ponds adjacent to Elkhorn Slough were the primary roosting areas for small shorebirds, American Avocets, and Black-bellied Plovers. Salt ponds in San Francisco Bay were similarly used by these species (Swarth et al. 1982). Seasonal changes in water depth reduce space available for resting or feeding in salt ponds (Swarth et al. 1982); rising water levels from winter rains restricted this space for small sandpipers in Elkhorn Slough. In general, little feeding took place in the salt ponds, but there were important exceptions.

Several uncommon species of shorebirds (e.g., phalaropes) roosted and fed exclusively in salt ponds. The salt ponds were not flushed by the tide during our surveys. However, when a major dike broke in 1984 and a large salt pond was exposed to tidal action, many shorebirds began to feed on the new intertidal mudflat.

The considerable variation in spatial and temporal use of habitat by a large variety of shorebirds within Elkhorn Slough and surrounding areas, and exchange of birds between these habitats, suggests that this wetland system is important to the viability of migrating shorebird populations. The intertidal mudflats can be regarded as critical and sensitive habitat for many of the shorebirds feeding in Elkhorn Slough during their annual migratory cycle. Degradation of this habitat could reduce the reproductive success and affect the survival of these populations.

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LITERATURE CITED

Baker, M. C., and Baker, A. E. M. 1973. Niche relationships among six species of shorebirds on their breeding ranges. Ecol. Monogr. 43:193–212.

Blick, D. J., Jr. 1980. Advantages of flocking in some wintering shorebirds. Ph.D. thesis, Univ. of Mich., Ann Arbor.

Broenkow, W. 1977. Water chemistry of Elkhorn Slough and Moss Landing Harbor, in Ecologic and Hydrographic Studies of Elkhorn Slough, Moss Landing Harbor and Nearshore Coastal Waters, July 1974–June 1976 (J. Nybakken, G. Cailliet, and W. Broenkow, eds.), pp. 388–465. Moss Landing Marine Laboratories, P. O. Box 450, Moss Landing, CA 95039.

Browning, B. M. 1972. The natural resources of Elkhorn Slough. Coastal Wetland Series 4, Calif. Dept. of Fish and Game.

Burger, J. 1984. Abiotic factors affecting migrant shorebirds, in Shorebirds: Migration and Foraging Behavior (J. Burger and B. L. Olla, eds.), pp. 1–72. Behavior of Marine Animals, vol. 6. Plenum, New York.

Burger, J., Howe, M. A., Hahn, D. C., and Chase, J. 1977. Effects of tide cycle on habitat selection and habitat partitioning by migrating shorebirds. Auk 94:743–758.

Connors, P. G., Myers, J. P., and Pitelka, F. A. 1979. Seasonal habitat use by Arctic Alaskan shorebirds, in Shorebirds in Marine Environments (F. A. Pitelka, ed.), pp. 101–111. Studies Avian Biol. 2.

Connors, P. G., Myers, J. P., Connors, C. S. W., and Pitelka, F. A. 1981. Interhabitat movements by Sanderlings in relation to foraging profitability and the tidal cycle. Auk 98:49–64.

Couch, A. B. 1966. Feeding ecology of four species of sandpipers in western Washington. M.S. thesis, Univ. of Wash., Seattle.

Gerstenberg, R. H. 1979. Habitat utilization by wintering and migrating shorebirds on Humboldt Bay, California, in Shorebirds in Marine Environments (F. A. Pitelka, ed.), pp. 33–40. Studies Avian Biol. 2.

Holmberg, N. D. 1975. The ecology of seven species of shorebirds (Charadrii) in north Humboldt Bay California, 1970–1971. M.S. thesis, Humboldt State Univ., Arcata, CA.

Jehl, J. R., Jr., and Craig, A. M. 1970. San Diego shorebird study. Spec. Wildlife Invest. Rept., Project W-54-R. Calif. Dept. of Fish and Game, Sacramento, CA 95814.

Jurek, R. M. 1974. California shorebird survey 1969–1974. Spec. Wildlife Invest. Rept. Project W-54-R, Job III-1. Calif. Dept. of Fish and Game, Sacramento, CA 95814.

Nybakken, J., and Jong, C. 1977. Benthic invertebrate baseline studies of the Moss Landing–Elkhorn Slough environment, in Ecologic and Hydrographic Studies of Elkhorn Slough, Moss Landing Harbor and Nearshore Coastal Waters, July 1974–June 1976 (J. Nybakken, G . Cailliet, and W. Broenkow, eds.), pp. 1–215. Moss Landing Marine Laboratories, P. O. Box 450, Moss Landing, CA 95039.

Page, G. W., and Stenzel, L. E. 1975. Aspects of the ecology of shorebirds on Bolinas Lagoon. Final Report to Dept. Parks and Recreation, County of Marin, 3501 Civic Center Drive, San Rafael, CA 94903-4177.

Page, G. W., Stenzel, L. E., and Wolfe, C. M. 1979. Aspects of the occurrence of shorebirds on a central California estuary, in Shorebirds in Marine Environments (F. A. Pitelka, ed.), pp. 15–32. Studies Avian Biol. 2.

Page, G. W., Shuford, W. D., Evens, J. G., and Stenzel, L. E. 1983. The distribution and abundance of aquatic birds in wetlands of the Point Reyes to Bodega area. A report for the Point Reyes–Farallones Marine Sanctuary. PRBO, 4990 Shoreline Hwy., Stinson Beach, CA 94970.

Page, G. W., Stenzel, L. E., Kjelmyr, J. E., and Shuford, W. D. 1990. Shorebird numbers in wetlands of the Pacific Flyway: A summary of spring and fall counts in 1988 and 1989. PRBO, 4990 Shoreline Hwy., Stinson Beach, CA 94970.

Pienkowski, M. W., and Evans, P. R. 1984. Migratory behavior of shorebirds in the western palearctic, in Shorebirds: Migration and Foraging Behavior (J. Burger and B. L. Olla, eds.), pp. 74–123. Behavior of Marine Animals, vol. 6. Plenum, New York.

Pinkas, L., Oliphant, M. S., and Iverson, I. L. K. 1971. Food habits of albacore, bluefin tuna, and bonito in California waters. Calif. Dept. of Fish and Game, Fish. Bull. 152:1–105.

Quammen, M. L. 1982. Influence of subtle substrate differences on feeding by shorebirds on intertidal mudflats. Marine Biol. 71:339–343.

Quammen, M. L. 1984. Predation by shorebirds, fish, and crabs on invertebrates in intertidal mudflats: An experimental test. Ecology 65:529–537.

Ramer, B. A. 1985. Seasonal abundance, habitat use, and diet of selected shorebirds in Elkhorn Slough. M.S. thesis, Moss Landing Marine Laboratories, Moss Landing, CA.

Recher, H. R. 1966. Some aspects of the ecology of migrant shorebirds. Ecology 47:393–407.

Reeder, W. G. 1951. Stomach analysis of a group of shorebirds. Condor 53:43–45.

Ruiz, G. M., Connors, P. G., Griffin, S. E., and Pitelka, F. A. 1989. Structure of a wintering Dunlin population. Condor 91:562–570.

Senner, S. E., and Howe, M. A. 1984. Conservation of nearctic shorebirds, in Shorebirds: Breeding Behavior and Populations (J. Burger and B. L. Olla, eds.), pp. 379–421. Behavior of Marine Animals, vol. 5. Plenum, New York.

Shuford, W. D., Page, G. W., Evens, J. G., and Stenzel, L. E. 1989. Seasonal abundance of waterbirds at Point Reyes: A coastal California perspective. W. Birds 20:137–265.

Sliger, M. C. 1982. Distribution and microhabitat selection of two grapsid crabs in Elkhorn Slough. M.S. thesis, Calif. State Univ., Hayward.

Smith, R. E. 1973. The hydrology of Elkhorn Slough, a shallow California coastal embayment. Moss Landing Marine Laboratories Tech. Publ. 73-2, P. O. Box 450, Moss Landing, CA 95039.

Speth, J. 1979. Conservation and management of coastal wetlands in California, in Shorebirds in Marine Environments (F. A. Pitelka, ed.), pp. 151–155. Studies Avian Biol. 2.

Stenzel, L. E., Huber, H. R., and Page, G. W. 1976. Feeding behavior and diet of the Long-billed Curlew and Willet. Wilson Bull. 88:314–332.

Stenzel, L. E., Page, G. W., and Young, J. 1983. The trophic relationships between shorebirds and their prey on Bolinas Lagoon. PRBO, 4990 Shoreline Hwy., Stinson Beach, CA 94970.

Stenzel, L. E., Kjelmyr, J. E., Page, G. W., and Shuford, W. D. 1989. Results of the first comprehensive shorebird census of northern and central California coastal wetlands 8–12 September 1988. Point Reyes Bird Observatory, 4990 Shoreline Hwy., Stinson Beach, CA 94970.

Swarth, C. W., Akagi, C., and Metropulos, P. 1982. The distribution patterns and ecology of waterbirds using the Coyote Hills salt ponds. San Francisco Bay Natl. Wildlife Ref., P. O. Box 524, Newark, CA 94560.

Townshend, D. J. 1981. The importance of field feeding to the survival of wintering male and female Curlews *Numenius arquata* on the Tees Estuary, in Feeding and Survival Strategies in Estuarine Organisms (N. V. Jones and W. J. Wolff, eds.), pp. 261–274. Plenum, London.

Wong, C. R. 1989. Observations of tides and tidal currents in Elkhorn Slough. M.S. thesis, Moss Landing Marine Laboratories, Moss Landing, CA.

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Are U.S. Regulations on Tuna-Dolphin Fishing Driving U.S. Seiners to Foreign-Flag Registry?

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Abstract.—From 1979 to 1988, the number of large purse-seiners (>400-tonne carrying capacity) in the U.S. tropical tuna fleet decreased by 35%, largely through sale and transfer of vessels to foreign registration. The U.S. regulations that protect mammalian dolphins associated with harvested schools of tuna are thought to be responsible for this switch to foreign-flag registration. A review of information on U.S. tuna–dolphin regulations, developments in the tuna industry, and dolphin kill data indicates that economic forces have been largely responsible for the reduction in the fleet and for vessels switching to foreign ownership and registration. The U.S. tuna–dolphin regulations played only a minor role, if any, and for the most part were not circumvented by vessels registering under flags of convenience.

Several species of dolphin, marine mammals sometimes called porpoises, associate with schooling tuna. Many dolphins have been killed when trapped in purse seines set around the tuna schools. The U.S. Government has regulated tuna fisheries since the early 1970s in an effort to reduce dolphin mortality. The press periodically prints claims that these regulations cause U.S. tuna seiners hardship and force them to register their vessels under foreign flags to stay in business. According to the press, this results both in less effective protection for dolphins of the eastern tropical Pacific Ocean (ETP) and in destruction of a healthy tuna industry.

Newspaper stories linking applications for foreign registry of U.S. tuna seiners to U.S. tuna–dolphin regulations have been widely circulated (Miller 1978; Griffin 1980). An American Tunaboat Association official, commenting on the switch of three U.S. seiners to foreign registry in April 1980, said that ". . . he believes government tuna–porpoise regulations and the growth of 200-mile limits in the tuna fishing grounds are big factors in the three boats leaving the U.S. fleet" (Griffin 1980).

The San Diego Tribune, in an editorial ("Shooting from the Hip," April 1, 1980) noted that ". . . clippers are switching to foreign registry to escape the restrictions [tuna–dolphin regulations] that the government already imposes on the American fleet but has no power to impose on competing foreign vessels."

Some researchers also have assumed that switching of registration is linked to restrictive measures on tuna–dolphin fishing. Andersen et al. (1978) examined the question of whether vessel transfers threatened the success of the U.S. dolphin protection efforts. However, they found a very low rate of purse-seine transfers from 1975 through 1977 and concluded that vessel transfers did not pose a threat.

Although these claims are generally accepted as

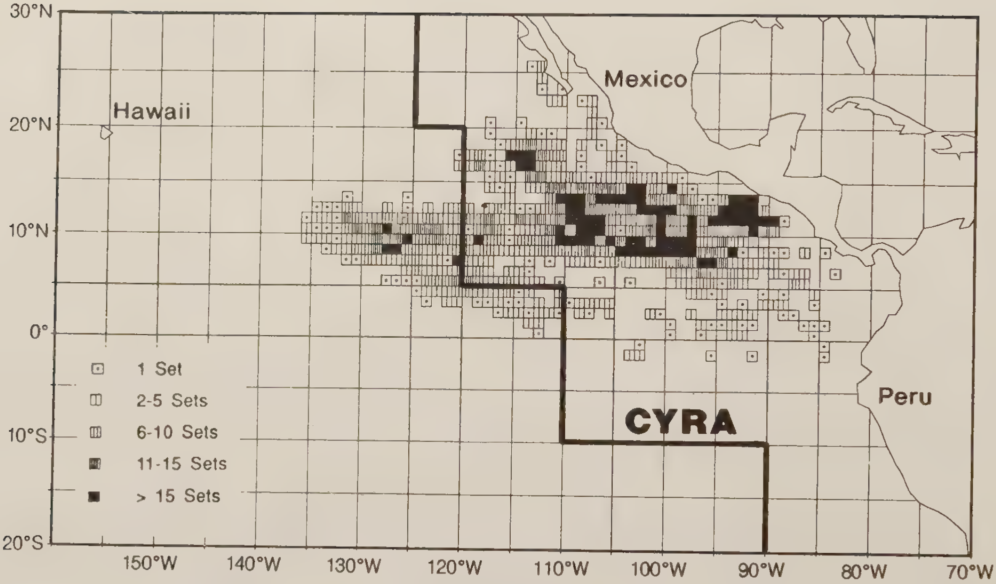

FIGURE 1.—Location and number of sets made on tuna–dolphin aggregations by U.S. purse-seiners in the eastern tropical Pacific Ocean in 1987, and the boundary of the Inter-American Tropical Tuna Commission's regulatory area (CYRA).

fact, they have not been substantiated with data. In this report I examine the claim that stringent U.S. tuna–dolphin regulations have been responsible for U.S. vessel transfers to foreign registry, particularly as a means for vessel owners to circumvent the regulations. My analysis is based principally on data accumulated through 1988.

The Record

Yellowfin tuna *Thunnus albacares* and skipjack tuna *Katsuwonus pelamis* occur in large schools, often together, in tropical and subtropical regions of the world oceans. They are caught with purse seines deployed by large, specially designed vessels. The catch, about 2.5 million tonnes in 1989, is used primarily in the international, multibillion-dollar tuna-canning trade (King 1987). Both species are canned as light-meat tuna, often commingled. However, yellowfin tuna is the premium light-meat species for canning because of its lighter color and larger size. Annually, the USA consumes 49% of the total world production of canned tuna, followed by western Europe (34%), Japan (7%), and other nations (10%).

Of the six principal tuna species in the world, only the yellowfin tuna is found to form close associations with dolphins (spotted dolphin *Stenella attenuata* and spinner dolphin *S. longirostris* primarily, but also common dolphin *Delphinus delphis,* striped dolphin *S. coeruleoalba,* and others). This symbiotic association usually involves large yellowfin tuna and dolphins. Only in the ETP is the association common and the bond so tight that herding the dolphins does not disrupt it—that is, the tuna continue to follow the surface-swimming dolphins (Perrin 1969; Green et al. 1971). Purse-seiners have used this bond in the ETP for catching yellowfin tuna since about 1959. Currently, fishing on tuna–dolphin schools produces about 70% of the total yellowfin tuna catch from the ETP (Figure 1).

The fishing process involves herding dolphins and yellowfin tuna with speedboats and helicopters, encircling the aggregation with a purse seine, releasing the dolphins from the net, and brailing the tuna aboard the vessel. In the process, some dolphins get entangled in the net and drown before they can be released (Barham et al. 1977). Dolphins most frequently killed by this fishery are the spotted and spinner dolphins (Smith 1983).

The incidental kill of dolphins by the ETP tuna fishery amounted to over 500,000 animals annually in the early 1960s and slightly less by the

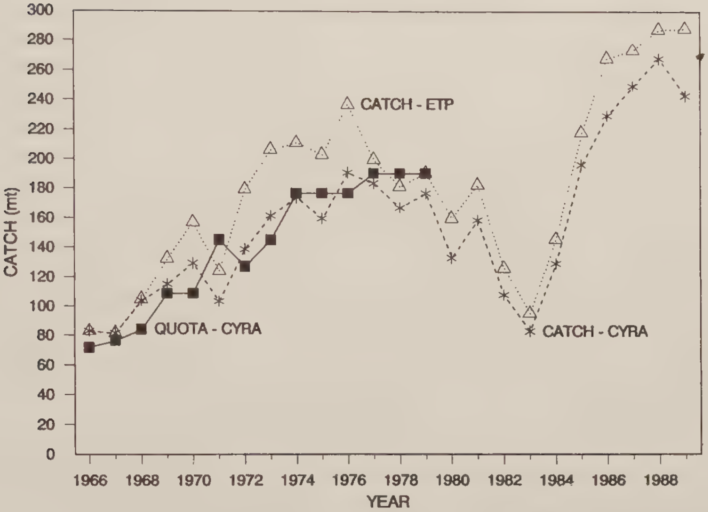

FIGURE 2.—Yellowfin tuna catch (metric tonnes) and quota for the regulatory area CYRA and for the eastern tropical Pacific (ETP) fishery. Since 1980, the fishery has not been under quota regulation.

late 1960s (Smith 1983). This high kill generated concern among conservationists and the public, who called for reforms through government regulations. The U.S. Congress responded by passing the Marine Mammal Protection Act (MMPA) in 1972 and reauthorizing the Act since then. Internationally, public concern caused the Inter-American Tropical Tuna Commission (IATTC) to accept responsibility, beginning in 1977, for scientific studies of dolphins and for providing dolphin-saving measures to fishermen involved in the tuna fishery under its authority.

International Tuna-Fishing Regulations

Only in the Atlantic Ocean and the ETP is fishing for yellowfin tuna regulated through international agreements. In the Atlantic, a minimum-size regulation of 3.2 kg has been in effect for yellowfin tuna since 1973. The regulation is administered by the International Commission for the Conservation of Atlantic Tunas (ICCAT), a 23-nation organization. This regulation has not had a significant effect on the conduct of the fishery, because enforcement by the fishing countries has been weak to nonexistent. Instead, canneries have discouraged landings of undersized fish by offering lower prices for small yellowfin tuna, which yield less canned product and cost more to process than large fish.

In the ETP, a more restrictive regulation—an annual catch quota—was used by IATTC to control the conduct of the yellowfin tuna fishery from 1966 through 1979, when it was suspended. The quota in 1966 was 71,900 tonnes for an area that paralleled the Latin American coast and extended several hundred kilometers offshore (Joseph 1970). This area referred to as the commission's regulatory area (CYRA), is shown in Figure 1. In subsequent years the quota gradually increased to a high of 190,500 tonnes (Figure 2) and the regulated area contracted slightly.

Major countries bordering the CYRA became dissatisfied with the IATTC quota system because it gave an advantage to the dominant U.S. fleet. Mexico withdrew from the IATTC in 1978 and Costa Rica followed in 1979. Both countries then took firm actions to restrict access of foreign fishing within their 370-km exclusive economic zones. Consequently, the IATTC management system became ineffectual and was suspended. Since 1979, the fishery has been operating without international controls, and the catch of yellowfin tuna in the CYRA has reached record highs of 268,500 tonnes in 1988 and 242,100 tonnes in 1989 (Figure 2). The yellowfin tuna stock, however, is currently in good condition (IATTC, unpublished data).

In 1977, the IATTC began promoting measures to avoid the needless killing of dolphins in the tuna fishery and to maintain ETP dolphin stocks at a high level in concert with high yield of tuna. So far, the IATTC has not instituted significant management measures to protect dolphins. In-

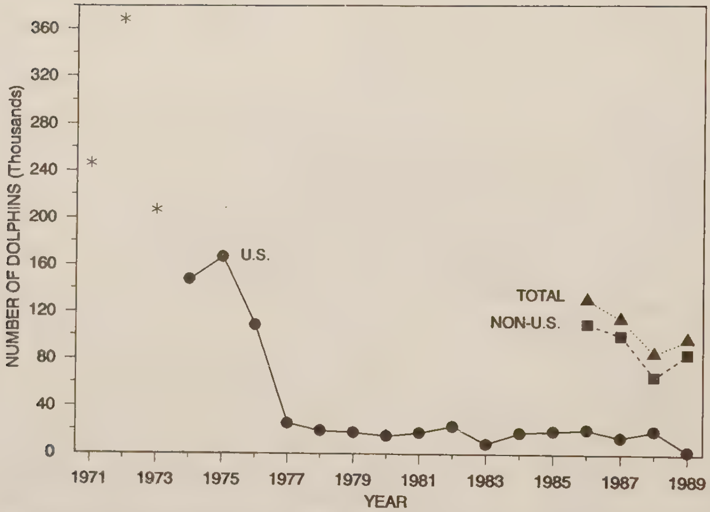

FIGURE 3.—Estimated number of dolphins killed by U.S. and non-U.S. purse-seine vessels participating in the eastern tropical Pacific tuna fishery. Although sampling by observers began in 1971 for the U.S. fleet and in 1983 for the non-U.S. fleet, coverage was not adequate until 1974 and 1986, respectively.

stead, it has concentrated on monitoring the kill with an international observer program that began in 1983, providing advice on available dolphin-saving gear and fishing procedures to fishermen, and conducting research on the condition of dolphin stocks. Despite these efforts, the annual incidental kill of dolphins in the ETP fishery has remained high (Figure 3).

U.S. Tuna–Dolphin Fishing Regulations

Since enactment of the MMPA in 1972, the U.S. tuna purse-seine fleet has been regulated for the protection of dolphins. Initially, regulations were nominal and consisted primarily of registration or certification requirements. Beginning in 1975, the regulations became more demanding as fishing gear, dolphin-saving procedures, and observer requirements were specified. Lawsuits and hearings delayed full implementation of those regulations until 1976 (Fox 1978). That year, after a judicial decision, the regulations took effect and a U.S. maximum-kill quota of 78,000 animals was added. In 1977, more procedural requirements were imposed, including the stationing of personnel with face masks in a rubber raft to aid in dolphin rescue during backdown and sacking of the net (Coe et al. 1984). Also, the kill quota was reduced to 62,429 animals (Figure 4). For 1978 through 1980, multiyear regulations were adopted. Regulations for this period were basically the same as for 1977 except for greater observer coverage and kill-quota reductions each year (Lo 1983). Starting in 1981, a 5-year requirement went into effect. The total U.S. kill quota was fixed at 20,500 animals per year, with special limits for some species and stocks. All fishing procedural regulations were relaxed to guidelines. In 1986 the regulations were extended for 2 years and observer coverage requirements were strengthened; full coverage (all fishing trips) was tested in 1987. In 1988, a 4-year extension of regulations was instituted. The kill quota of 20,500 animals per year remained, full observer coverage was mandated, restrictions were placed on sundown sets (sets that extend into night) as well as on the use of seal bombs (explosives similar to firecrackers but more powerful) for scaring fish and dolphins, and kill-rate performance standards were mandated for captains.

These measures contributed to a substantial reduction in the incidental dolphin kill. In 1975, the total incidental kill of dolphins by U.S. tuna purse-seiners was estimated at 166,600 animals; by 1977, the total had decreased sharply and was well below the quota (Figure 4). In 1989, an estimated 12,600 dolphins were killed by the U.S. tuna purse-seine fleet in the ETP; in contrast, the non-U.S. fleet killed an estimated 84,300 dolphins (Figure 3).

The MMPA also prescribes requirements that indirectly affect foreign purse-seiners that catch tuna associated with dolphins. The act allows for

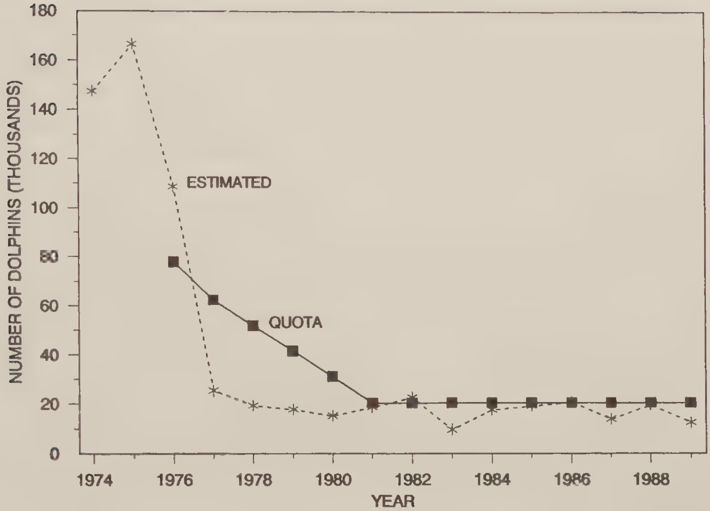

FIGURE 4.—Dolphin kill quota and estimated incidental kill of dolphins by U.S. purse-seiners participating in the eastern tropical Pacific tuna fishery. Annual kill quotas started in 1976.

U.S. sanctions against noncomplying countries that export tuna and tuna products to the USA. Before 1986 the requirements were light. Foreign governments only had to certify that dolphin protection measures were practiced by their fleets. Countries were encouraged to participate in the IATTC tuna–dolphin program as a means of satisfying the requirements. In 1988, U.S. regulations were tightened to allow imports of yellowfin tuna and tuna products only if the exporting country documented its fleet's compliance with requirements similar to MMPA requirements for the U.S. fleet. In addition the foreign fleet's average kill rate at the end of 1989 had to be no more than two times the U.S. rate; by 1990, it could be no more than 1.25 times the U.S. rate.

U.S. Tuna-Processing Sector

Since 1972, the U.S. tuna industry has undergone significant changes aside from adjusting to regulations specified by the MMPA. Most significant was the restructuring of the processing sector during 1979–1985. Owing to U.S. consumer resistance to purchases of high-priced canned tuna in 1979–1980 and a change in consumer preference from tuna packed in oil to tuna packed in water, processors pursued means to reduce production costs and modify production capability (Herrick and Koplin 1984). Marginal plants, particularly continental U.S. operations, were closed and offshore capacity was expanded to take advantage of greater resource availability, lower labor costs, and tax benefits (USITC 1986). Labor cost, for example, was substantially lower in Puerto Rico and American Samoa than in California. In 1985, the hourly wage for entry-level tuna cannery workers was US$3.35–4.40 in Puerto Rico and $2.94 in American Samoa (USITC 1986). In contrast, it was $6.63 in California. Tax laws also are more favorable in Puerto Rico and American Samoa than in the continental USA. Both Puerto Rico and American Samoa provide generous special exemptions from their tax laws to tuna canneries. In addition, income derived by canners is exempt from U.S. corporate income tax.

The most publicized cannery closures were the Bumble Bee Seafoods plants in San Diego, California (1982), and Honolulu, Hawaii (1984); the Van Camp Seafoods plant in San Diego (1984); and the Star-Kist Seafoods plant in Terminal Island, California (1984). Expansion or improvements to plants in American Samoa and Puerto Rico were made by Van Camp Seafoods and Star-Kist Seafoods beginning in 1985.

Restructuring of the processing sector also took the form of increased reliance on low-cost foreign sources for preprocessed raw material—that it, tuna loins—and for finished canned products (Doulman 1989). In 1979 the USA imported 2.75 million standard cases (48 6.5-ounce cans per case) of canned tuna from foreign sources. By 1985 the volume had tripled to 10.97 million cases (S. Her-

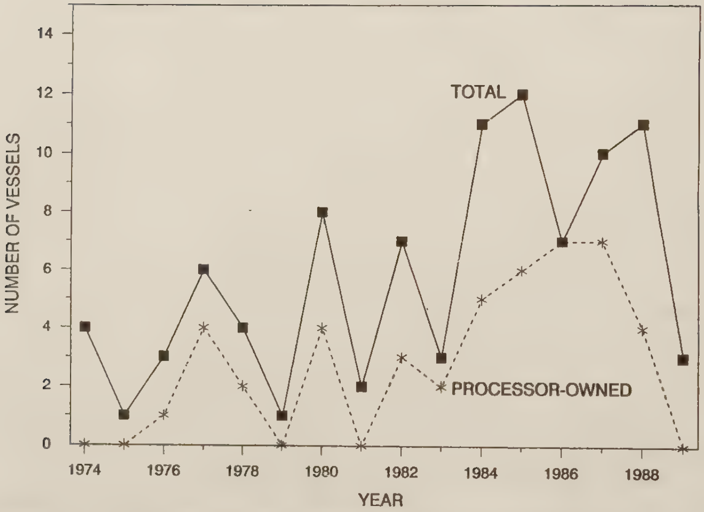

FIGURE 5.—Number of U.S. tuna purse-seiners that transferred to foreign-flag registration, and number owned (majority ownership) by U.S. processors.

rick, Southwest Fisheries Science Center, personal communication), and the trend has continued upward to a record-setting 17.90 million cases in 1989. Restructuring culminated in the sale of Van Camp Seafoods in 1988 and Bumble Bee Seafoods in 1989 to foreign processors, P.T. Mantrust of Indonesia and Unicord Co. of Thailand, respectively.

Before 1981 it was common for processors to own and operate tuna vessels, often in partnership with operating captains. This promoted close captain–processor ties that guaranteed a steady supply of tuna for the processors and operating capital and profit for the captains. However, when foreign countries began expanding their tuna fleets in the late 1970s, U.S. processors recognized that the increased supply of low-cost raw tuna gave foreign processors a competitive edge (USITC 1986; FNI 1988). So U.S. processors bought more raw tuna from foreign sources at low prices and less of the higher-priced domestic supply. Many U.S. vessels had to suspend fishing because the low prices were well below levels that could sustain costs of ownership and operation (Davis 1983). More than 20% of the U.S. fleet was tied up at the docks during all or part of 1982–1984. Many of these vessels were owned entirely or in partnership by the processors, and they went up for sale as the processors began divesting their interest in vessels (Figure 5). Orders for construction of new U.S. tuna seiners also came to a halt.

Foreign investors with lower operating costs (D. Doulman, Forum Fishery Agency, personal communication) and expanding interests in high-valued tuna fisheries for the export market began purchasing used U.S. tuna vessels. From 1978 to 1982, purchases and transfers were principally to Mexican interests (45%). From 1983 to 1987, most (42%) purchases were by Venezuelan interests. Since 1987, Korean investors have been actively involved in purchases and transfers.

Some of these transfers did not meet sales agreements and eventually reverted back to U.S. ownership and registry. However, the net result, including transfers to U.S. non-tuna fisheries and a few new additions, was a reduction in the U.S. fleet from about 101 active large purse-seiners (>400-tonne carrying capacity) in 1979 to 66 vessels in 1988, a 35% decreases.

U.S. Tuna-Harvesting Sector

Closure of major processing plants in the continental USA, as well as changes in availability of tuna and in the Law of the Sea (Joseph and Greenough 1979), also brought about changes in the U.S. tuna-harvesting sector. During the 1970s, the U.S. fleet depended principally on stocks in the ETP and marginally on stocks in the eastern tropical Atlantic (ETA) off Africa. Catches were landed primarily in California and Puerto Rico, where U.S. processors bought virtually all landings for canning purposes.

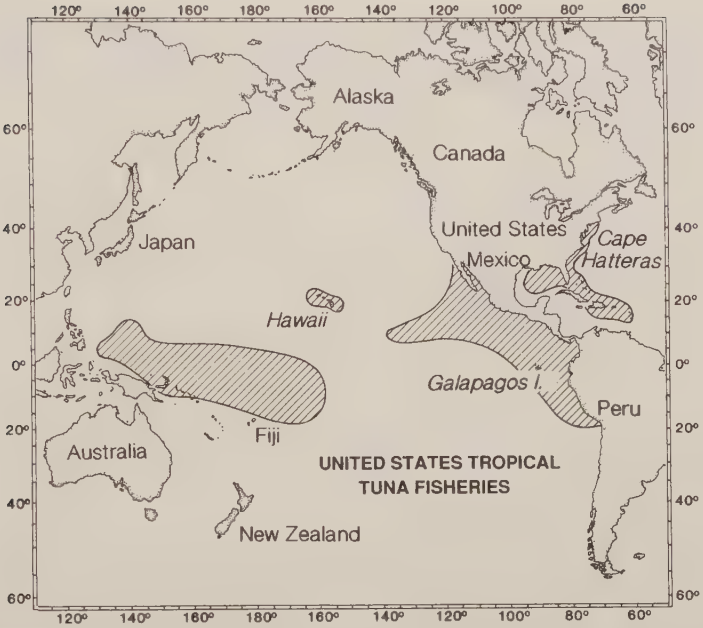

FIGURE 6.—Location of U.S. fisheries for tropical tunas (yellowfin and skipjack). U.S. tuna purse-seiners currently operate in the eastern tropical Pacific off Mexico to Peru and in the central-western Pacific southwest of Hawaii.

Changes in the Law of the Sea prompted coastal states bordering the rich tuna-fishing areas to establish 370-km (200-nautical-mile) extended jurisdiction during the mid-1970s. This made it difficult for the U.S. fleet to gain reasonable access to productive, inshore fishing areas. Also, during the late 1970s, the catch rate for the premium species, yellowfin tuna, was at record low levels in the ETP owing to overexploitation. Logistical support for U.S. vessels in the ETA was hindered by political unrest in Africa and increased competition with foreign fleets, principally of France and Spain. So U.S. vessels withdrew completely from the ETA in 1981 and concentrated their fishing in the ETP. This increased U.S. presence (95 large U.S. vessels in 1981) came at a time when Latin American countries began expanding their fleets in the ETP, which created considerable strain on the resource. An alternative fishing area was needed to draw off some of the fishing capacity.

Exploitation of the central-western Pacific Ocean (Figure 6) with its large stock of skipjack tuna began in earnest during the mid-1970s (Felando 1987). At first, traditional purse-seine fishing techniques did not work. New gear and methods had to be developed and mastered for the region. By 1980 the gear and methods were refined enough for vessels to operate profitably, and participation increased as vessels shifted from the ETP (Figure 7). The most significant shift occurred in 1982–1984, when the ocean condition known as El Niño caused catch rates to plummet in the ETP and to increase in the central-western Pacific. In 1988 slightly less than half of the U.S. fleet (29 of 66

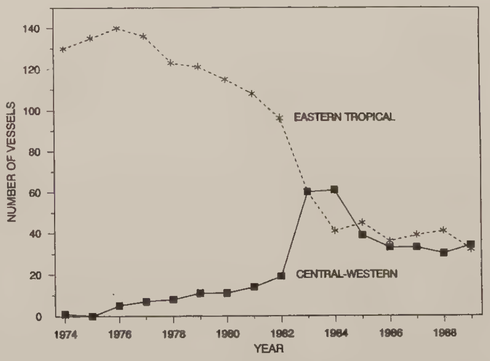

FIGURE 7.—Number of tuna purse-seiners in the eastern tropical and central-western Pacific fisheries by year. Numbers are based on fishery participation during the fourth quarter of each year, so few vessels were double-counted because they fished in both fisheries during a year.

TABLE 1.—Number of vessels by designated country of reregistration for U.S. tuna purse-seiners transferring out of the U.S. fleet. Some vessels reverted back to U.S. registration and were involved in more than one transaction.

Country of reregistration	Year, 19 . . 74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	Total
Venezuela							1	1		1	5	2	6	4	1	21
Mexico	2		2		1		5		4		1			1		16
South Korea							1		2					1	7	11
Chile											3	4				7
Vanuatu												3	1	2		6
Cayman Islands							1	1			1	1				4
Panama				2						1				1		4
Philippines	1				1	1			1							4
Costa Rica				2	1											3
Netherlands Antilles				2	1											3
Japan												2				2
Mauritania															2	2
Australia											1					1
Canada		1														1
France															1	1
India														1		1
New Zealand			1													1
Peru	1															1
Taiwan										1						1
Total	4	1	3	6	4	1	8	2	7	3	11	12	7	10	11	90

vessels) operated in the central-western Pacific (Figure 7); their catch was landed or transshipped to canneries principally in American Samoa. The other half operated in the ETP and landed catches for canneries principally in Puerto Rico. In 1988 the U.S. fleet caught 124,600 tonnes of tuna from the central-western Pacific and 123,800 tonnes from the ETP.

The Analysis

Data on transfers of U.S. tuna purse-seiners by year to foreign registry were tabulated from records submitted by vessel owners to the U.S. Coast Guard and from sources in the U.S. tuna industry. The records do not always designate the flag country for reregistration or the exact year of occurrence; consequently, the tabulated data by year and country are approximations (Table 1). Also, two or three vessels were involved in repeat transactions in different years when the original transactions failed.

Information on whether a vessel transfer included flag as well as management control was obtained from industry sources: virtually all transfers included both. Most of the flag countries involved in reregistration required a minimum of 51% ownership and control of the property by their citizens to qualify for flag registration. Furthermore, U.S. tuna vessel owners had no tradition of using flags of convenience. Their vessels were built and financed in the USA, where they qualified for benefits (USITC 1986) that would be forfeited with foreign registration.

Transfers of U.S. tuna seiners to foreign registry were no more than six per year from 1974 through 1984 (Table 2; Figure 5). Eight vessels transferred in 1980, when tuna consumption in the USA stalled, prices fell, and restructuring of the U.S. tuna industry commenced. Processors began liquidating their holdings in vessels and initiated other cost-cutting measures. Transfers again became more frequent after 1981, reaching highs of 12 vessels in 1985 and 11 in 1988; most of these vessels were processor-owned.

The U.S. maximum-kill quota for dolphins declined between 1976 and 1981 and remained constant at 20,500 animals thereafter (Figure 4). Fishing procedural regulations were very severe during 1978–1980 but less severe during 1980–1988. Despite these regulations, the U.S. fleet operated within the dolphin quota except for 2 years (Figure 4).

The relationship between the dolphin quota, a nominal measure of severity of tuna–dolphin regulations, and the number of vessel transfers is poor; there is an overall upward trend in number of transfers during 1979–1988 when the quota was constant.

The number of transfers appears to be more directly linked to economic factors. For instance, the upward trend of transfers occurred during a period when overall economic conditions and prof-

TABLE 2.—Statistics on number of U.S. tuna purse-seiners by carrying capacity that transferred to foreign registration, nominal ex-vessel price of yellowfin tuna paid to U.S. fishermen, and average per-vessel profit (loss) for the U.S. tuna purse-seine fleet.

Year	Number of vessels: Small (<400 tonnes)	Large (>400 tonnes)	Total	Price of yellowfin tuna[a] (US$/ tonne)	Average profitability[b] (thousands of US$)
1974	3	1	4		
1975	1	0	1		
1976	0	3	3		
1977	0	6	6		
1978	0	4	4		
1979	0	1	1		(202)
1980	0	8	8	1,070	(43)
1981	0	2	2	1,061	(340)
1982	0	7	7	1,018	(691)
1983	0	3	3	936	(463)
1984	3	8	11	891	(111)
1985	4	8	12	744	(588)
1986	0	7	7	674	
1987	0	10	10	809	
1988	0	11	11		

[a] Nominal ex-vessel price per tonne of yellowfin tuna for 1980–1987 from S. Herrick (Southwest Fisheries Science Center, personal communication).

[b] Average profit (loss) per vessel for 1979–1985 from USITC (1986).

itability of U.S. tuna vessels were poor, and when the industry underwent restructuring. During 1982–1984, a significant portion of the U.S. fleet was tied up, primarily because of weak tuna prices and the high cost of servicing capital debt (Davis 1983). Marginal vessels went out of business and the remaining ones reported net losses, on the average (Table 2). The correlation between net losses and number of transfers for 1979 through 1985 is not significant ($r = 0.66$, df = 5; Figure 8). However, the correlation between number of transfers and nominal ex-vessel prices of yellowfin tuna (Table 2) is significant ($r = 0.87$, df = 6; Figure 9). In other words, when the ex-vessel price of yellowfin tuna was high, few vessels switched to foreign flags; when the price was low, many vessels switched. In reality yellowfin tuna prices and other economic factors—including tax incentives and debt service costs—were probably involved in vessel transfer or investment decisions.

Although tuna–dolphin regulations did not appear to play a significant role in vessel transfer decisions, there is a hint that perhaps they played a secondary role in affecting which flag countries were involved in the transfers. Prior to about 1981, Mexico adhered to the IATTC yellowfin tuna quota system, expanding its fleet and freely exporting its catch to the USA. During this period a large proportion (37%) of transfers of U.S. tuna vessels went to Mexico (Table 1). Then, in 1980, Mexico seized a U.S. tuna seiner for fishing in an area not recognized by the United States as belonging to Mexico, and the USA placed an embargo on imports of Mexican tuna. Mexico also declined to participate in the IATTC tuna–dolphin program or to provide adequate documentation for MMPA requirements, which precipitated an additional

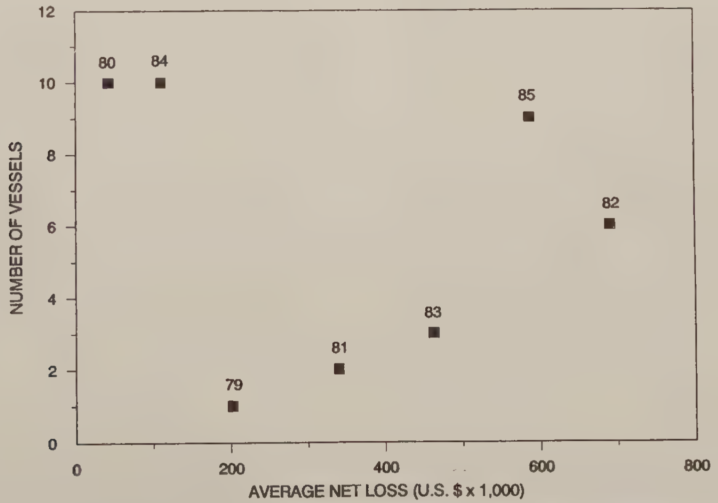

FIGURE 8.—Relationship between number of U.S. vessels transferred to foreign-flag registration and average net economic loss (thousands of US$) of U.S. purse seiners, 1979–1985. Year is shown for each point.

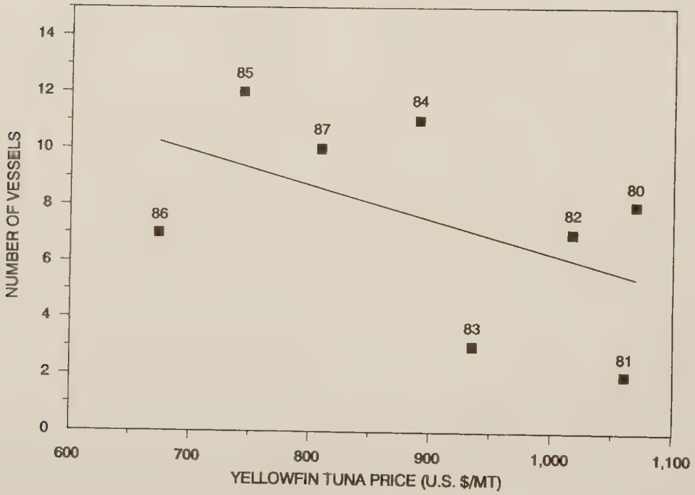

FIGURE 9.—Relationship between number of vessels (Y) transferred to foreign registration and nominal U.S. ex-vessel price (X, US$/metric tonne) for yellowfin tuna, 1980–1987. Year is shown for each point along with the linear regression line, $Y = 18.48 - 0.012X$.

embargo. Not until 1986, when Mexico joined the IATTC tuna–dolphin program, were the embargoes lifted. During the 1981–1986 embargo period, only five transfers (12%) were made to Mexico. Venezuela, on the other hand, which met MMPA requirements and freely exported tuna to the USA, became the home for 15 former U.S. vessels (36%) during this period.

The future outlook is for transfer of fewer U.S. vessels, and most of those will be older or smaller vessels too costly to own and operate under U.S. registry or from a U.S. port. This forecast is based on changes in vessel ownership, market conditions, and regulations.

During 1979–1987, 56% of the transferred vessels were owned by processors, either solely or with a majority share (Figure 5). Those processors liquidated virtually all of their vessel holdings to generate capital for restructuring. Now, the liquidation has been largely completed and processors have a significantly lower capital involvement in the U.S. harvesting sector. Remaining active vessels in the U.S. fleet are mostly owned and operated by U.S.-based families with a long allegiance to tuna fishing. They are less likely to liquidate their holdings en masse as did processors in the early 1980s.

The economic climate for vessel operators as a whole has improved. There are firmer markets, slower growth in operating costs (particularly in debt service), and higher catch rates in the ETP. Also operators can fish in the central-western Pacific under the South Pacific Tuna Treaty, a treaty between the USA and 16 south Pacific island countries that permits up to 50 U.S. purse-seiners access to tuna in the region. This has allowed most vessel owners to operate profitably, to consider construction of more efficient replacement vessels (FNI 1988), and to exploit more options for fishing strategy.

Changes in the MMPA in 1988 now require all foreign countries that export yellowfin tuna and fish products to the USA to adopt comparable tuna–dolphin regulations. Moreover, these exporters must include a schedule for reducing their dolphin kill rate to a level comparable to U.S. vessel performance, and they are required to impose trade sanctions ("secondary" sanctions) on trading partners who fish for yellowfin tuna but do not adopt U.S.-type tuna–dolphin regulations. The MMPA regulations are thus written to reduce any competitive advantage that a foreign-registered purse-seiner may have over a U.S.-registered vessel in marketing yellowfin tuna caught in association with dolphins.

Recent Events

On April 12, 1990, the three largest tuna processors in the USA (Star-Kist Seafoods, Van Camp Seafoods, and Bumble Bee Seafoods), which together account for 80% of domestic production, pledged to stop buying or selling tuna caught in a manner that kills or injures dolphins. This pledge in effect terminates virtually all U.S. purse-seine deliveries of ETP tuna to U.S. processors, because most of the U.S. catch from the ETP fishery is taken on dolphins, the preferred manner of fishing for that region (Jackson 1989).

In the months ahead, the full effect of this pledge will be unfolding. It is already clear, however, that the U.S. purse-seine fleet will be deeply affected. There will be a reduction of U.S. vessels participating in the ETP fishery and an increase in vessels participating in the central-western Pacific fishery. Also, some vessels will explore means of participating in the Atlantic or Indian Ocean fisheries. The full 50 licenses allowed under the South Pacific Tuna Treaty have already been subscribed by vessels switching or planning to switch from the ETP fishery. About 14 purse-seiners continue to fish in the ETP, but this number is expected to shrink, given increased costs to market their catch, softening of prices for ETP tuna, and increased competition for schools of tuna not associated with dolphins. Several particularly small and older vessels have suspended their ETP operations and are for sale. A few of these vessels no doubt will be sold to foreign investors and registered under foreign flags.

This event underscores the influence of market forces on the U.S. tuna industry in general and the U.S. tuna purse-seine fleet in particular. The downsizing of the U.S. purse-seine fleet and the transfer of U.S. vessels to foreign flags in the 1980s occurred because of changes in the economic climate of the industry, not because of government tuna–dolphin regulations. The transfers were the result of the sale of vessels to foreign interests and not a ploy to circumvent U.S. tuna–dolphin regulations.

Acknowledgments

The complex, emotionally charged tuna–dolphin issue has many facets, from biology to politics; consequently, I relied on many individuals for information, advice, and comments. Assistance is acknowledged from the following colleagues: Norman Bartoo, Atilio Coan, and Sam Herrick (Southwest Fisheries Science Center, La Jolla); Svein Fougner, Lt. James Herkelrath, Rodney McInnis, and J. Gary Smith (Southwest Region, Terminal Island); Michael Hinton (IATTC, La Jolla); and Bernard Fink (Van Camp Seafoods, San Diego). The dedicated efforts of National Marine Fisheries Service tuna–dolphin observers in collecting data used in this study are also acknowledged.

References

Andersen, S. O., R. C. Anderson, and B. J. Searles. 1978. The tuna–porpoise dilemma: is conflict resolution attainable? Natural Resources Journal 18:505–519.

Barham, E. G., W. K. Taguchi, and S. B. Reilly. 1977. Porpoise rescue methods in the yellowfin purse seine fishery and the importance of the Medina panel mesh size. U.S. National Marine Fisheries Service Marine Fisheries Review 39(5):1–10.

Coe, J. M., D. B. Holts, and R. W. Butler. 1984. The "Tuna–Porpoise" problem. NMFS dolphin mortality reduction research, 1970–1981. U.S. National Marine Fisheries Service Marine Fisheries Review 46(3):18–33.

Davis, J. 1983. West Coast focus: no place to go but up after dismal '82 season for California tunamen. National Fisherman (April):7.

Doulman, D. J. 1989. Recent developments in the U.S. canned tuna market. INFOFISH International 6(89): 12–17.

Felando, A. 1987. U.S. tuna fleet ventures in the Pacific Islands. Pages 93–104 *in* D. J. Doulman, editor. Tuna issues and perspectives in the Pacific Islands region. East–West Center, Honolulu, Hawaii.

FNI (Fishing News International). 1988. Costly to rebuild U.S. fleet. Fishing News International (October):12–14.

Fox, W. W., Jr. 1978. Tuna/dolphin program—five years of progress. Sea Sense (May):57–59.

Green, R. E., W. F. Perrin, and B. P. Petrick. 1971. The American tuna purse seine fishery. Pages 3–15 *in* H. Kristjonsson, editor. Modern fishing gear of the world 3. Fishing News Books, London.

Griffin, V. 1980. Three more U.S. tuna boats to switch flags. San Diego Tribune, April 1, 1980, p. A-14.

Herrick, S. F., Jr., and S. Koplin. 1984. U.S. tuna trade summary, 1983. U.S. National Marine Fisheries Service Marine Fisheries Review 46(4):65–72.

Jackson, A. R. 1989. Summary of the 1987 U.S. tuna–porpoise observer data. NOAA (National Oceanic and Atmospheric Administration) Technical Memorandum, NMFS (National Marine Fisheries Service) NOAA-TM-NMFS-SWFC-136, Southwest Fisheries Science Center, La Jolla, California.

Joseph, J. 1970. Management of tropical tunas in the eastern Pacific Ocean. Transactions of the American Fisheries Society 99:629–648.

Joseph, J., and J. W. Greenough. 1979. International management of tuna, porpoise, and billfish. University of Washington Press, Seattle.

King, D. M. 1987. Global tuna markets: a Pacific Island perspective. Pages 279–298 *in* D. J. Doulman, editor. Tuna issues and perspectives in the Pacific Islands region. East–West Center, Honolulu, Hawaii.

Lo, N. C. H. 1983. Sample size for estimating dolphin mortality associated with the tuna fishery. Journal of Wildlife Management 47:413–421.

Miller, W. C. 1978. U.S. tunaboats begin move to secure foreign registry. National Fisherman (January): 12A.

Perrin, W. F. 1969. Using porpoise to catch tuna. World Fishing 18(6):43–45.

Smith, T. D. 1983. Changes in size of three dolphin (*Stenella* spp.) populations in the eastern tropical Pacific. U.S. National Marine Fisheries Service Fishery Bulletin 81:1–13.

USITC (U.S. International Trade Commission). 1986. Competitive conditions in the U.S. tuna industry. USITC, Publication 1912, Washington, D.C.

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MESOSCALE OCEANIC RESPONSE TO WIND EVENTS OFF CENTRAL CALIFORNIA IN SPRING 1989: CTD SURVEYS AND AVHRR IMAGERY

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ABSTRACT

Analysis of hydrographic data obtained during juvenile groundfish surveys, in relation to local wind forcing and AVHRR sea-surface temperature imagery, reveals that the oceanic region off central California between Point Reyes and Point Sur in spring 1989 was characterized by complex circulation patterns and considerable temporal and mesoscale variability. The "spring transition" to upwelling-favorable winds is most clearly evidenced by rapid, large decreases in SST (up to 4°–5°C) measured at four meteorological buoys. Daily-averaged winds are spatially coherent and oscillate between upwelling-favorable and relaxation conditions at 3–10-day intervals.

Persistent upwelling centers near Point Reyes and Point Año Nuevo were characterized by relatively cool, salty (8°–10°C, 33.6–34.0 psu) water in the upper 50 m, which is derived from offshore water at depths of 50–100 m. Water-mass analysis reveals that upwelled water is advected equatorward from its source. Some upwelled water is transported into shallow coastal areas and warmed. Alongshelf fronts between relatively warm, low-salinity (>13°C, <33.5 psu) offshore water and cool, higher-salinity upwelled water are advected onshore in response to wind relaxation or reversal events; frontal gradients intensify at these times. AVHRR imagery verifies the spatial patterns and complex mesoscale variability of the near-surface patterns observed in the CTD survey data. Eddylike hydrographic features are noted with horizontal scales on the order of the station spacing (10 km). How the complex circulation patterns and intense mesoscale spatial and temporal variability affect the survival and subsequent recruitment of juvenile groundfish is discussed.

RESUMEN

Análisis de datos hidrográficos con relación a la fuerza del viento local y a imágenes infrarrojas de satélite (AVHRR SST), obtenidos durante las campañas de investigación de juveniles de peces de fondo, muestra que la región oceánica de la parte central de California, entre Punta Reyes y Punta Sur, en la primavera de 1989, estaba caracterizada por patrones de circulación complejos y una considerable variabilidad temporal y espacial de mediana escala. La "transición de primavera" hacia vientos favorables a la surgencia de aguas es claramente evidente en las grandes y rápidas reducciones en salinidades y temperaturas superficiales (SST), de hasta 4°–5°C, medidas entre cuatro boyas meteorológicas. Los promedios diarios de los vientos son coeherentes en el espacio y varían entre condiciones favorables a la surgencia y períodos de relajamiento en intervalos de 3 a 10 dias.

Centros de surgencia persistentes cerca de Punta Reyes y Punta Año Nuevo estaban caracterizados por aguas relativamente frías y saladas (8°–10°C, 33.6–34.0‰) en los 50-m superficiales. Esta agua se deriva del mar abierto a profundidades de 50–100 m. Análisis de masas de aguas muestran que el agua de surgencia se desplaza hacia el ecuador desde su punto de origen. Algo de agua de surgencia es transportada hacia zonas costeras poco profundas donde se calienta. Frentes a lo largo de la plataforma continental, que separan aguas de mar abierto relativamente cálidas y de baja salinidad (>13°C, <33.5‰) y aguas de surgencia frías y de más alta salinidad, son desplazados hacia la costa en respuesta al relajamiento de los vientos (o sucesos revertidos); los gradientes a través del frente se intensifican en estos momentos. Imágenes de satélite infrarrojas verifican los patrones espaciales y la compleja variabilidad de las aguas superficiales observada en escalas intermedias con sonda de temperatura, salinidad, y profundidad (CTD) durante las campañas. Se observaron rasgos hidrográficos parecidos a remolinos con escalas horizontales del orden de la distancia entre estaciones (10 km). Se discute la influencia de los patrones complejos de circulación y la intensa variabilidad temporal y espacial a escalas intermedias con relación a la supervivencia y reclutamiento de los juveniles de los peces de fondo.

INTRODUCTION

The oceanic region off central California between Point Reyes (38°N) and Point Sur (36.3°N) (figure 1) is characterized by several important dynamic processes and features that contribute to an ap-

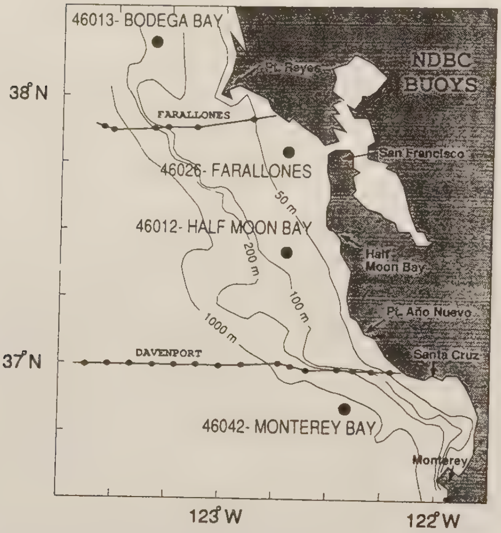

Figure 1. Area map of the juvenile rockfish recruitment survey region, showing location of NDBC meteorological data buoys (*large solid circles*) and cross-shelf CTD sections.

parently complex circulation. Significant physical processes include wind-forced motions (e.g., upwelling, horizontal advection, vertical mixing), tides, the circulation of the large-scale California Current system, flow/bathymetry interactions, and buoyancy effects (e.g., heat exchange with the atmosphere, freshwater inflow). Bathymetric features on a range of scales that could profoundly influence the circulation appear throughout the region. These include submarine canyons, banks, seamounts, headlands and embayments of various dimensions, and a wide range of continental shelf and slope widths. Water masses of unique characteristics may enter the region via local upwelling, advection onshelf or alongshelf due to changes in wind stress, and freshwater discharge, primarily from San Francisco Bay. Given this complex arrangement of forces and processes, a circulation that varies greatly in time and space should be expected over this portion of the California shelf.

This coastal environment is also a transition zone between two major biogeographical provinces, resulting in the presence of more species than are found either in the cold-temperate north (Oregonian Province, 35°–55°N) or in the warm-temperate south (California Province, 25°–35°N) (Briggs 1974). The area around Monterey Bay is believed to be a distributional barrier for a variety of marine organisms, including algae (Murray et. al. 1980), molluscs (Valentine 1966), and fish (Horn and Allen 1978). The rich biological diversity may be enhanced further by the complex circulation patterns and by the diverse physical processes and variety of water types and ocean conditions in the region. At least, the flow regime must greatly influence the location, temporal variability, and ultimate success of larval and juvenile dispersal and recruitment into the adult groundfish population.

The region features numerous commercially and recreationally important species of groundfish, including the *Sebastes* complex—a major component of the West Coast groundfish fishery (Gunderson and Sample 1980), with annual landings from 1981–88 averaging over 45,000 MT/yr (PFMC 1989). Since 1983, the Southwest Fisheries Science Center (SWFSC) of NOAA NMFS has conducted a systematic midwater trawl field survey of the coastal ocean between Point Reyes and Point Sur each spring. The goals of the survey are to describe variations in groundfish recruitment, and to define the environmental conditions that lead to variability within the fishery. Data obtained during these annual surveys provide information on distribution and abundance patterns of young-of-the-year pelagic juveniles in this area (Wyllie-Echeverria et al. 1990). The Groundfish Analysis Group of SWFSC Tiburon Laboratory, under the direction of William Lenarz, is developing a recruitment index for rockfish based on this information.

The physical oceanographic component of these annual studies includes repeated surveying of the central California coastal region's hydrography via conductivity/temperature/depth (CTD) vertical casts and continuous surface mapping of temperature and salinity. CTD data from three spring 1989 sweeps (NOAA R/V *David Starr Jordan* cruise DS89-04) are used to define and describe the predominant hydrographic features present in the near-surface coastal ocean off central California following the spring transition. Selected Advanced Very High Resolution Radiometer (AVHRR) satellite sea-surface temperature (SST) images are used to verify and test the synopticity of the maps constructed from near-surface ship observations and to detail surface hydrographic features occurring beyond the sampling region.

We will discuss two key hypotheses. First, hydrographic and circulation features off central California, on scales on the order of 100 km, occur persistently during the upwelling season. Second, substantial spatial (10–50-km) and temporal (1–2-day) variations occur in the position and extent of these features. We focus on defining persistent hydrographic features and their variability on synoptic (<10-day) time scales. These should relate to natural fluctuations within the physical processes (e.g., upwelling) that control the circulation and, ultimately, the distribution and eventual settlement of larval and juvenile groundfish.

METHODS

Juvenile Rockfish Survey Design

Annual 30-day cruises aboard the NOAA R/V *David Starr Jordan* began in 1983 and have been conducted annually during late spring (May–June), a time when most pelagic stage juvenile rockfishes are identifiable to species, but before they settle to nearshore and benthic habitats. The sampling design presently permits three consecutive sweeps through a study area from 38°10′N (near Point Reyes) and 36°35′N (near Monterey), and from the coast to about 75 km offshore (figure 1). A CTD cast is made at each trawl station. Beginning in 1987, daytime activities were restructured to permit sampling of a more extensive grid of CTD stations. Each sweep is sampled south to north, and takes approximately ten days (seven nights of scheduled work plus three nights of additional discretionary sampling).

Collection and Processing of CTD Data

All CTD data obtained during the 1989 juvenile rockfish surveys were collected with a Sea-Bird Electronics SEACAT-SBE-19 profiler. At each CTD station, the profiler was lowered to its maximum rated depth (200 m), or to a depth 10 m off the bottom if water was less than 200 m deep. Only data collected on the downcast were ultimately preserved for analysis. A total of 380 acceptable CTD casts were obtained during the 1989 survey. One hundred thirty-five acceptable casts were obtained during sweep 1 (14–22 May); 153 casts during sweep 2 (23 May–3 June); and 92 casts during sweep 3 (4–13 June). Schwing et al. (1990b) provide a detailed description of the data collection and the reduction and processing procedures for this cruise, together with a full suite of data.

Meteorological Time Series

Meteorological data were obtained for selected sites in the survey region (figure 1). These sites include the region's four National Data Buoy Center (NDBC) moored buoys—46013 (Bodega Bay: 38.2°N, 123.3°W); 46026 (Farallones: 37.8°N, 122.7°W); 46012 (Half Moon Bay: 37.4°N, 122.7°W); and 46042 (Monterey Bay: 36.8°N, 122.4°W)—and a land station at Monterey (Monterey Bay Aquarium; 36.6°N, 121.9°W). Daily averages of several surface meteorological characteristics, including air and sea temperature, wind speed and direction, and barometric pressure, were calculated for the period that includes the 1989 *Jordan* rockfish survey. The principal axis components of each buoy's wind, which is the compass heading along which variance is maximized, were also derived.

AVHRR Imagery

Sea-surface temperature (SST) images for the study region were produced from the data of the AVHRR carried aboard TIROS-N/NOAA polar-orbiting satellites (McClain et al. 1985). The calculated SST values and the blackbody brightness temperatures were registered to the surface temperature at NDBC 46042. Additional processing details are found in Tracy 1990.

RESULTS

Meteorological Conditions Preceding and During the DS89-04 Cruise

Meteorological time series of the daily vector mean wind, the principal axis component of the wind, and SST are presented for the four NDBC buoys (figures 2 and 3). All four NDBC wind series display very similar signals. Daily winds at Monterey Bay Aquarium are included to demonstrate the relative difference in wind speed over land and ocean. Until about 1 May, there were frequent (every 3 to 10 days) reversals or reductions in the principal wind component; however, the mean alongshore wind was about zero. After 1 May, winds at all sites were predominantly southward to southeastward (i.e., upwelling-favorable), until 30 June and beyond. This dramatic change in the region's wind patterns, called the spring transition (Huyer et al. 1979; Lentz 1987; Strub et al. 1987b), marks the onset of the upwelling season. However, numerous wind-relaxation events (reductions in the speed of upwelling-favorable wind) and wind-reversal events occurred during the upwelling season (Send et al. 1987). Two notable reversals occurred near the beginning of sweeps 2 (23 May) and 3 (4 June). Although the principal component at the three southern buoys is nearly alongshore, thus optimal for upwelling, the principal axis at Bodega is nearly normal to the coast (figure 2).

The synoptic variability of the wind field is reflected in SST at the buoys as well (figure 3). Changes in SST were relatively minor before the spring transition, and were associated with wind

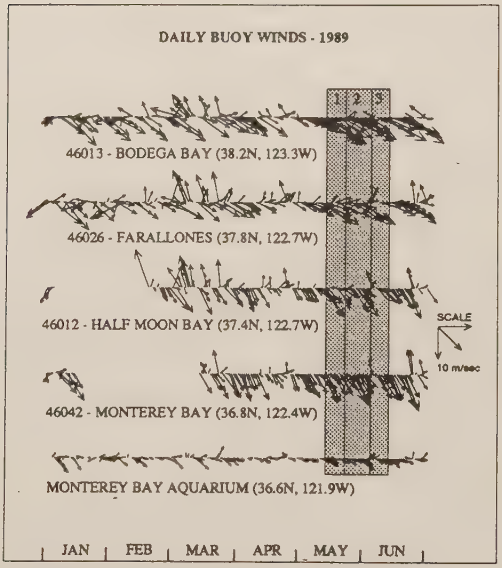

Figure 2. Vector time series of daily average winds from NDBC buoys and Monterey Bay Aquarium, January–June 1989. *Arrows* point in direction to which wind was blowing. *Shaded area* denotes period of groundfish cruise.

reversals. SST was also positively correlated with air temperature (not shown) at each site. The onset of upwelling, however, resulted in a dramatic decrease in SST of up to 4°–5°C at the buoys. Wind reversals and relaxations are reflected as warming events in the SST signals. Although SST at all four buoys responded similarly to wind forcing, the magnitude of the response, as well as the mean temperature for the upwelling season, varied with location. Monterey SST is generally the warmest; Bodega is generally the coolest.

In summary, both wind and SST from NDBC buoy time series varied widely on scales less than 10 days; i.e., less than the period of one sweep. For example, buoy SSTs changed by as much as 3°C during a single sweep. Such variability must be kept in mind for interpretations of the "synoptic" horizontal property maps from a single sweep—especially near-surface conditions, which are most influenced by meteorological forcing.

Horizontal Maps of Temperature, Salinity, and Density

Near-surface (5-m-depth) temperature and salinity throughout the groundfish survey region is summarized, by sweep, in a series of horizontal maps (figures 4–6). These maps were objectively contoured from the CTD cast data. The NDBC SST and principal wind-component time series, shown as inserts in the temperature maps, clearly demonstrate that conditions changed substantially during the course of each sweep. We will consider day-to-day environmental changes when describing the hydrography, rather than interpret the contour maps in a synoptic sense, i.e., as if the entire survey was made instantaneously.

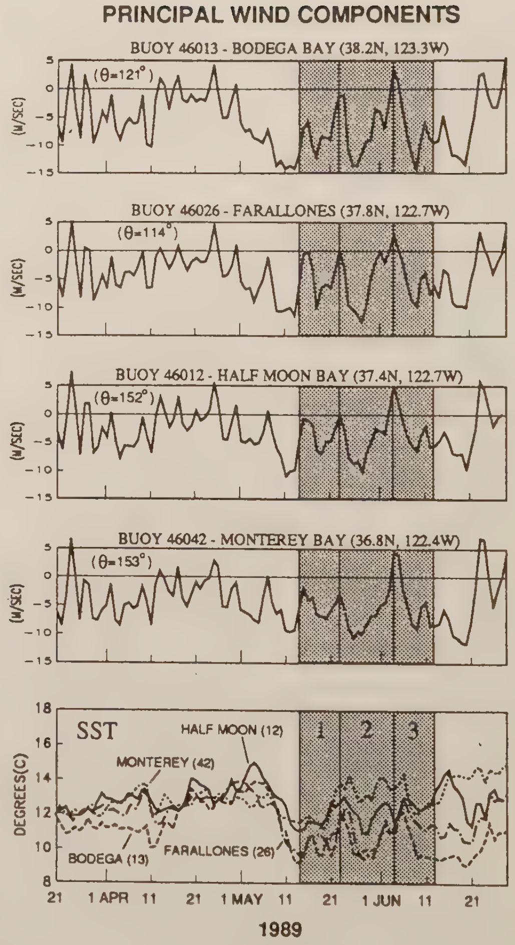

Figure 3. Time series of principal-axis wind component and sea-surface temperature (SST) from NDBC buoys for 21 March–29 June 1989. Negative wind speeds are in the direction of the principal axis, defined by θ at each buoy. *Shaded areas* denote period of groundfish cruise.

Sweep 1 surface hydrography. Near-surface conditions during sweep 1, 14–22 May (figure 4), reflect

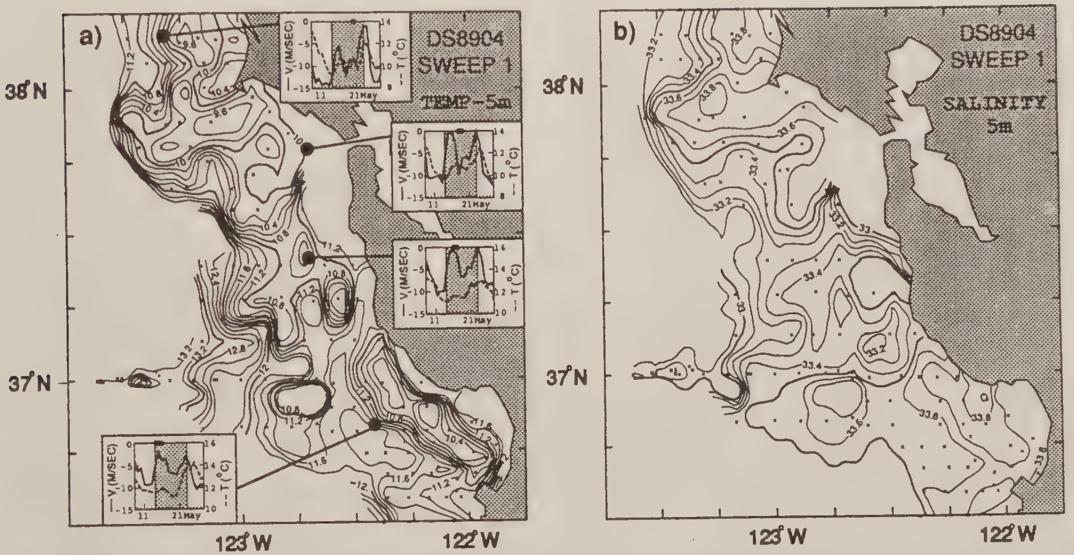
a)
DS8904
SWEEP 1
TEMP-5m
b)
DS8904
SWEEP 1
SALINITY
5m
38°N
37°N
123°W
122°W
V (M/SEC)
T (°C)
11
21May

Figure 4. *a*, Temperature at 5-m depth during sweep 1 (14–22 May 1989), from CTD data. Location of CTD stations denoted with an x. Contour interval is 0.2°C; *bold contours* denote 1°C intervals. Time series of principal-axis wind components and SST at the four NDBC buoys, whose positions are denoted by *large solid circles*, are also shown. *Shaded areas of buoy records* define sweep duration; *short bold bars* mark period when stations in the area of each buoy were occupied. *b*, Salinity at 5-m depth during sweep 1. Contour interval is 0.1 psu; *bold contours* denote 0.5-psu intervals.

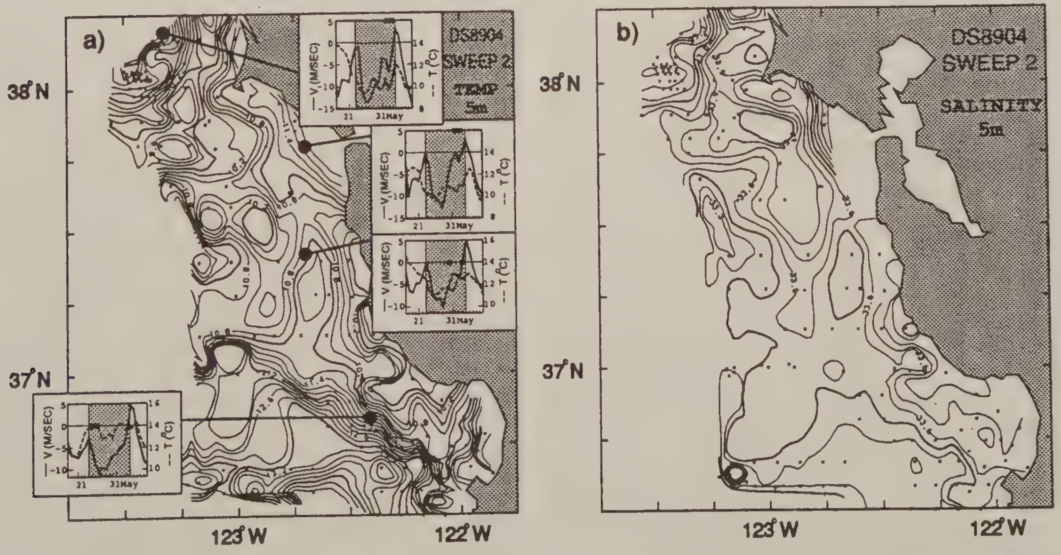
a)
DS8904
SWEEP 2
TEMP
5m
b)
DS8904
SWEEP 2
SALINITY
5m
38°N
37°N
123°W
122°W
V (M/SEC)
T (°C)
21
31May

Figure 5. *a*, Temperature at 5-m depth during sweep 2 (23 May–3 June 1989), from CTD data. Contour interval is 0.2°C; *bold contours* denote 1°C intervals. See figure 4a for further details. *b*, Salinity at 5-m depth during sweep 2. Contour interval is 0.1 psu; *bold contours* denote 0.5-psu intervals.

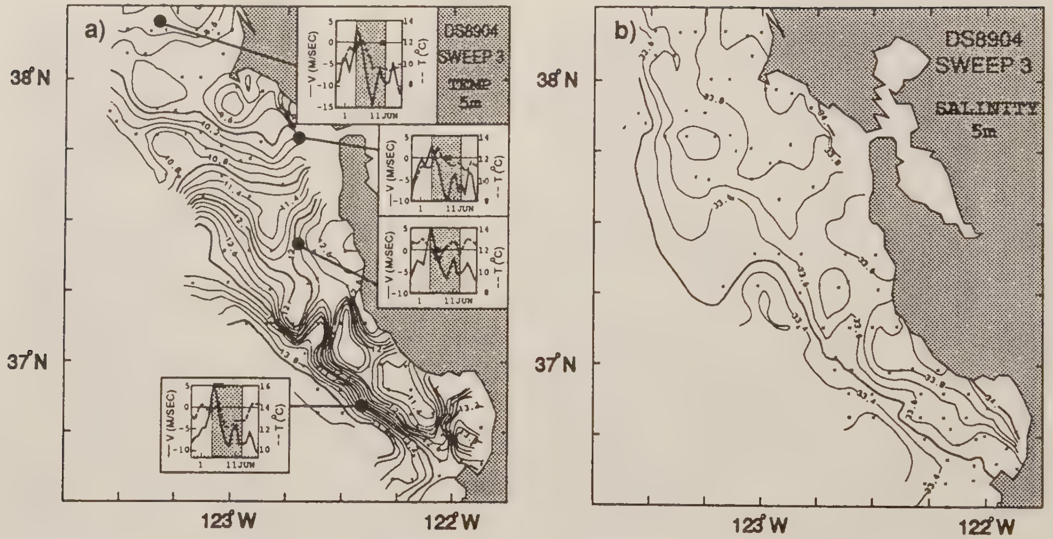

Figure 6. *a*, Temperature at 5-m depth during sweep 3 (4–13 June 1989), from CTD data. Contour interval is 0.2°C; *bold contours* denote 1°C intervals. See figure 4a for further details. *b*, Salinity at 5-m depth during sweep 3. Contour interval is 0.1 psu; *bold contours* denote 0.5-psu intervals.

the presence, position, and extent of several features of water mass and circulation typically seen in this region during spring. Two relatively cool (<10.5°C) and saline (>33.7 psu) areas of recently upwelled surface water appear near Point Reyes (38.0°N) and Point Año Nuevo (37.2°N). These areas of upwelled water contrast with the much warmer (>13°C) and less saline (<33.0 psu) surface water seen offshore. A warm feature that appears persistently west of Monterey Bay in CTD maps and AVHRR SST imagery (Tracy 1990) is composed of this water type. A strong alongshelf front often develops between these two water types. A second source of warm, fresh water appears to be the San Francisco Bay plume; however, CTD coverage is limited in the area where the bay's effluent is most evident. The plume is more apparent in AVHRR imagery.

Situated within these larger water masses are numerous mesoscale eddylike features whose horizontal dimensions are on the order of 10 km. They are much smaller than previous hydrographic sampling in the region (e.g., CalCOFI) could reveal, and are barely resolvable at the station spacing of the rockfish surveys. The existence and size of these features are confirmed with continuous surface mapping (Schwing et al. 1990b) and AVHRR imagery.

The coolest and most saline water was observed during sweep 1 off Point Reyes, and featured a minimum temperature of about 9.5°C and a maximum salinity of over 33.9 psu. This water was bounded offshore by a very strong front. Surface water gradually increased in temperature and decreased in salinity from Point Reyes to Half Moon Bay. A second relatively cool, saline feature extended along the shelf from Point Año Nuevo to near Monterey, crossing the mouth of Monterey Bay. Tracy (1990) demonstrated the existence of a persistent upwelling center off Point Año Nuevo with AVHRR imagery. His results imply that upwelled water is subsequently advected south in a relatively shallow (<50 m) surface layer toward Monterey Bay. The position and extent of the elongated cool, salty feature seen in figure 4 is consistent with those findings. A similar process, associated with an upwelling center north of the survey region, is probably responsible for the cool, saline water seen near Point Reyes.

Although the highest salinities within these recently upwelled features were observed at sites nearest the coast, the coolest water was actually found about 20–25 km offshore. Thus the shallowest portions of the shelf adjacent to these upwelling sources feature relatively warm and saline water at the surface. The discrepancy is more extreme off Point Año Nuevo and in Monterey Bay. In contrast, temperatures at 30 m (not shown) were coolest at the most nearshore sites, corresponding to the salinity maximum at this depth. The character of this coastal water suggests that it was upwelled, then warmed over the shallow (<50 m) areas of the shelf. Aside from this difference in shallow shelf regions, the surface hydrographic features seen in all three sweeps extended to 50 m and deeper.

Sweep 2 surface hydrography. Near-surface temperature and salinity patterns during sweep 2, 23 May–3 June (figure 5) are similar to those seen during sweep 1. The coolest and most saline water masses were located off Point Reyes and Point Año Nuevo; warmer, fresher water was noted again in the offshore and southern portions of the region and immediately seaward of San Francisco Bay. Again the fine scale of the sampling design reveals several mesoscale hydrographic features. However, temperature, salinity, the position and extent of these water types, and the location and intensity of the fronts that separate them all vary substantially from sweep 1. For example, the offshore front during sweep 1 was sharper north of 37°N than to the south. During sweep 2 this front was much more distinct south of 37°N. The Point Año Nuevo upwelling center featured a cooler minimum temperature (<10°C) during sweep 2, and was constrained to the shallowest stations along the coast. The maximum salinity near Point Año Nuevo was also higher (>34 psu) during sweep 2.

Stations off Point Año Nuevo and Half Moon Bay were occupied after a significant wind-relaxation event during sweep 1, but after relatively strong upwelling-favorable winds during sweep 2. Stations off Monterey, on the other hand, were surveyed after the upwelling-favorable conditions that preceded the first survey, but immediately following the significant wind-relaxation event of 23 May. Thus it appears that a stronger offshore front develops during relaxation events, in contrast with the findings north of Point Reyes (Send et al. 1987).

Sweep 3 surface hydrography. Conditions during sweep 3, 4–13 June (figure 6), display even more dramatic differences from the first two sweeps, although the same water masses and eddylike features are again apparent. The alongshelf front separating upwelled and offshore water masses is sharpest off Monterey Bay; essentially no cross-shelf gradient is seen north of 37.5°N. Surface water south of 37°N was 1°–2°C warmer during sweep 3, with the coolest water (11.5°C) away from the coast once again. Stations in the southern half of the survey were occupied after a strong wind reversal; northward wind components up to 5 m/s were observed at all buoys on 4 June. As a result, the offshore front was most distinct during this sweep.

Temperature-Salinity Relationships

A temperature-salinity diagram composed of CTD observations taken south of 37.25°N during sweep 2 clearly defines the differences between the offshore, upwelled, and nearshore water masses, and reveals some of the region's vertical structure (figure 7). Surface offshore water (*triangles*; >13°C, 33.2–33.4 psu) contrasts with water at upwelling centers north of Monterey Bay (*circles*; <10.5°C, 33.6–33.9 psu). These two masses are separated by an alongshore front, represented by *diamonds*. Frontal water comprises a linear mixture of offshore and upwelled water. Upwelled water at the surface displays the characteristics of offshore water at 50-m depth. In addition, upwelled water at 50 m is similar to the 100-m offshore water; i.e., water is vertically advected by about 50 m near the coast. Nearshore water, confined to Monterey Bay in this area, features salinities identical to those measured at upwelling centers, but is 1°–2°C warmer. The range of temperature and salinity, defined at the surface, 50 m, 100 m, and 200 m within dashed lines, decreases with depth. The large temperature range observed at the surface is probably due to greater short-term variability in surface heating.

Individual profiles of temperature, salinity, and density from stations representing offshore, upwelled, nearshore, and frontal locations (figure 8) further reveal the distinct characteristics of these water masses. Although the temperature of nearshore water to about 60 m was between that at offshore and upwelling sites, its salinity was clearly that of the upwelling centers. At greater depths, the salinity in Monterey Bay is increasingly that of an offshore source. Frontal water, in contrast, is some mixture of offshore and upwelled water to at least 150 m.

AVHRR SST

Four SST images (figure 9) collected during the survey period provide an excellent illustration of how quickly the position, extent, and intensity of surface water masses can change. Both the persistence of features and the variability of their relative locations are demonstrated in these data. The observed patterns correspond closely with those described from the hydrography. All are presented with the same grey scale, which is linear between 8° and 13°C. Waters cooler than 8°C are uniformly light; waters warmer than 13°C are uniformly dark.

The first image, from 11 May, shows the SST pattern three days before the beginning of sweep 1. This image was collected just before the peak of a fairly strong period of upwelling-favorable winds. Cool

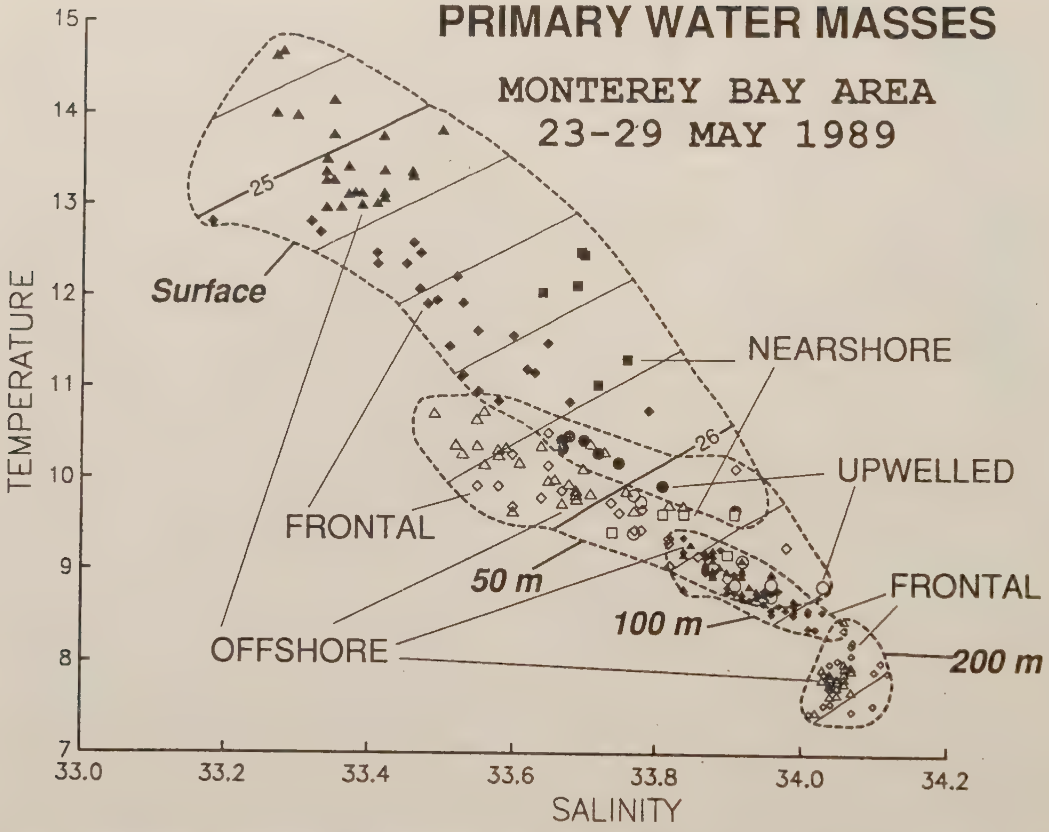

Figure 7. Temperature-salinity (T-S) diagram from CTD observations taken south of 37.25°N during sweep 2. *Dashed lines* enclose T-S ranges at surface (*large solid symbols*), 50-m depth (*large open symbols*), 100-m depth (*small solid symbols*), and 200-m depth (*small open symbols*). *Triangles* represent T-S pairs at offshore stations; *circles* represent stations in upwelling centers; *squares* represent nearshore (Monterey Bay) stations; and *diamonds* represent frontal stations. Sigma-t isolines are shown at 0.2 kg/m³ intervals.

water (lighter shade) extends south past Point Reyes to about 37.25°N. It appears that this streamer comprises cool water upwelled from two sources. The majority is an extension of cool water from the north, flowing past Point Reyes, and augmented by water upwelled locally near the point. South of 37.5°N, the streamer separates, one portion going approximately alongshelf southeast of 123°W, the other passing offshore to the southwest. Warmer water (darker shade) is located between these streamers.

A warm streamer, with maximum temperature offshore of the Golden Gate, extends to the south, leaving the coast around Half Moon Bay. Cool water, suggestive of coastal upwelling, appears along the coast from Half Moon Bay to Santa Cruz and again to the south of Monterey Bay. This cool water band appears separated from the Point Reyes cool water by the Golden Gate warm band.

The cool upwelling streamer near Point Año Nuevo has offshore and alongshore components and the suggestion of a warm feature between them, similar to the streamer off Point Reyes. The alongshore streamer extends south from Santa Cruz about halfway across Monterey Bay. Surface temperature inside the bay is fairly uniform, with the suggestion of some warm water right along the coast. Clouds obscure the southwest corner of the image.

This image corresponds well with the sweep 1 surface map (figure 4a). The Point Reyes streamer and the downstream split are clearly seen, as well as

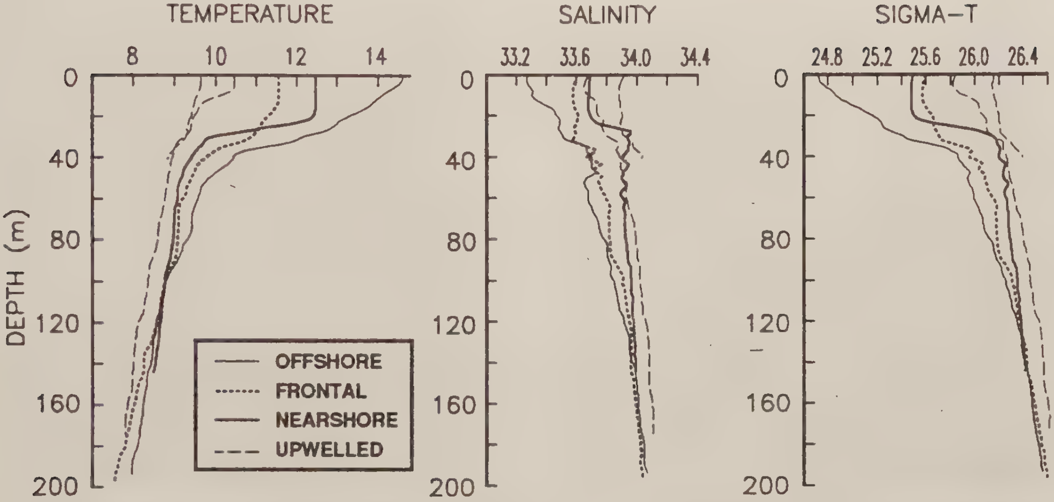

Figure 8. Individual profiles of temperature, salinity, and sigma-t at CTD stations representative of offshore, upwelled, nearshore, and frontal locations during sweep 2.

the Point Año Nuevo streamer extending across Monterey Bay, and the relatively warm water inside the bay. The position of the alongshelf front separating upwelled and offshore water is also approximated. Although the eddylike features seen in the CTD near-surface maps appear in the AVHRR imagery as complex but connected flow features, the small spatial scales of variability noted in the hydrographic data are reflected in the satellite observations.

The date of the second image, 25 May, is closer to the time of the northern sampling during sweep 1 (19–21 May) than sweep 2 (1–3 June). The southern portion of the study area was surveyed during sweep 2 at the time of this image, thus that portion of figure 5a has a slightly stronger correspondence to figure 9b. Upwelling-favorable winds began blowing on 24 May, following a significant wind reversal. Although the general pattern is the same, the SST field on 25 May differs from that on 11 May (figure 9a) in two significant ways. The most noticeable change from sweep 1 is the presence of a distinct warm feature just west of Monterey Bay. Although this feature looks like a meander or eddy at this scale, the full-scale image (not shown) suggests that it is best described as a warm segment of the variegated eastern boundary of the California Current. In addition, the whole region appears slightly warmer relative to two weeks earlier.

The Point Reyes streamer is still well defined on 25 May, extending south to the edge of the warm feature off Monterey Bay (figure 9b). However, it is not as cool as that seen after several days of upwelling-favorable wind (cf. figure 9a). The streamer is no longer divided, although the offshore edge shows evidence of complex small-scale interaction with the warmer oceanic water to the west. The Golden Gate warm streamer again extends south, separating the Point Reyes streamer from the cool coastal water present from Half Moon Bay to Santa Cruz. Distinct cool water centers are seen along this portion of the coast. Cool water extends across Monterey Bay; the separation of warm coastal (Monterey Bay) water from the warm offshore feature is more distinct than noted previously. As in the sweep 2 surface-temperature map (figure 5a), the strongest front is associated with the north-to-southeast edge of this feature. There are no strong fronts in the northern part of the study area, although remnants of the different water masses are seen.

By 28 May (figure 9c) the coastal oceanic response to the upwelling event that began about 24 May is well established. There is strong upwelling both north and south of Point Reyes, near Point Año Nuevo, and near Point Sur. Water from these upwelling centers has spread both offshore and generally southward. The coastal-oceanic boundary has retreated offshore. This is demonstrated by the

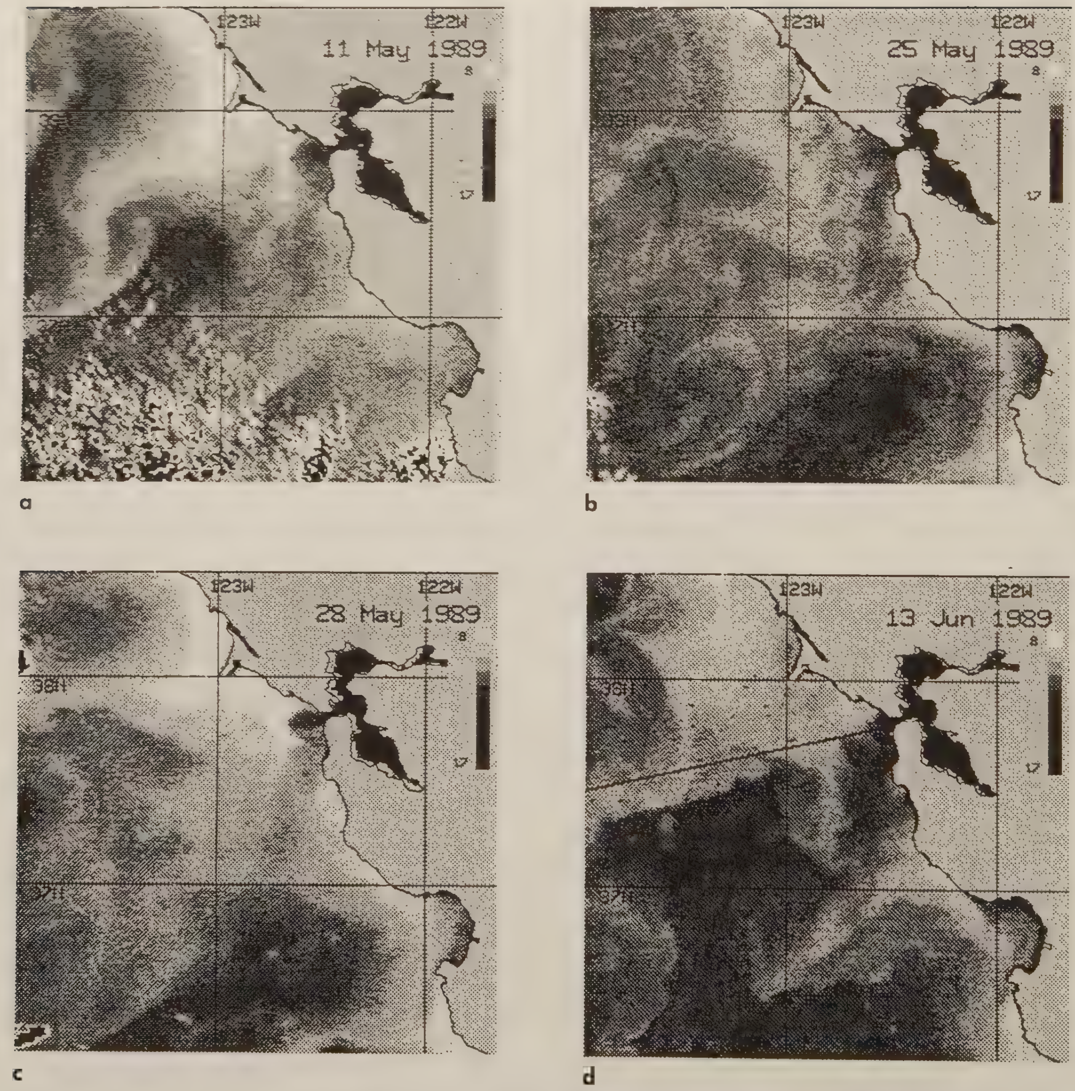

Figure 9. AVHRR sea-surface temperature (SST) images of the survey region from 11 May, 25 May, 28 May, and 13 June 1989. Linear grey scale for SST is shown. Lighter shades denote cooler temperatures. Speckled pattern at bottom of image from 11 May is scattered cloud. Latitude and longitude are shown at 1° intervals.

westward displacement of the warm water off Monterey Bay. A comparison of the images in figures 9b and c, taken only three days apart, clearly shows how suddenly and dramatically coastal ocean conditions can change during the upwelling season.

About two weeks later, 13 June, the imagery reveals more warm water closer to shore, with coincident warming and possible constriction of the southward-flowing Point Reyes cool streamer (figure 9d). Winds at this time were light and upwelling-favorable, but varied substantially from north to south (figures 2 and 3). There is again an offshore streamer of cool water west of Point Año Nuevo, possibly comprising both Point Año Nuevo and

Point Reyes cool waters. But the offshore extent of this cool water is limited, relative to that during upwelling periods. During strong wind reversals, such as on 29 June (figures 2 and 3), surface evidence of upwelling is hidden as the entire coastal region warms to greater than 13°C (Tracy 1990).

The Point Reyes streamer appears ~2°C warmer than the Point Año Nuevo coastal upwelling streamer on 13 June, probably because the northern portion of the survey region was under wind-relaxation conditions while the southern part was experiencing stronger southward wind (figure 2). The warm feature off Monterey Bay is still present, and is connected with a region of warm water extending northward, west of 123°W. This image further indicates the complexity of the boundary between the coastal and offshore water masses. The warmest water is seen again off the Golden Gate and in Monterey Bay. Figure 9d corresponds well with the CTD temperature map from sweep 3 (figure 6a), even though the image was taken on the last day of the sweep.

The impression gained from a series of satellite images of the study area is that several general water masses, indicated by surface temperature, are present at all times, but their relative and absolute location can change on short subsynoptic time scales not detected by traditional ship-survey methods. These changes could profoundly affect the biota in the region, as discussed below.

Both the persistence of these water masses during the upwelling season, and their variability on synoptic time scales is reflected in the CTD surface maps (figures 4–6) as well as the NDBC SST time series (figures 2 and 3). The consistently coolest buoy site, off Bodega, is located near the core of the southward-flowing upwelling streamer off Point Reyes. Buoy SST increases to the south, as this streamer mixes with warmer surrounding water. The warmest buoy, off Monterey, lies in the warm feature that separates the two Point Año Nuevo upwelling streamers.

Vertical Cross-Shelf Sections

The vertical distribution of density along two representative cross-shelf sections (figure 1), extending offshore from Davenport (37°00′N) and through the Farallones (37°53′N), are presented for each sweep in figures 10 and 11. These figures display the vertical structure and extent of the features defined previously from the near-surface CTD and AVHRR data. They also show the pronounced spatial and temporal variability of the coastal ocean associated with upwelling/relaxation events. The time series of the principal-axis wind component from the NDBC buoy nearest each section is included.

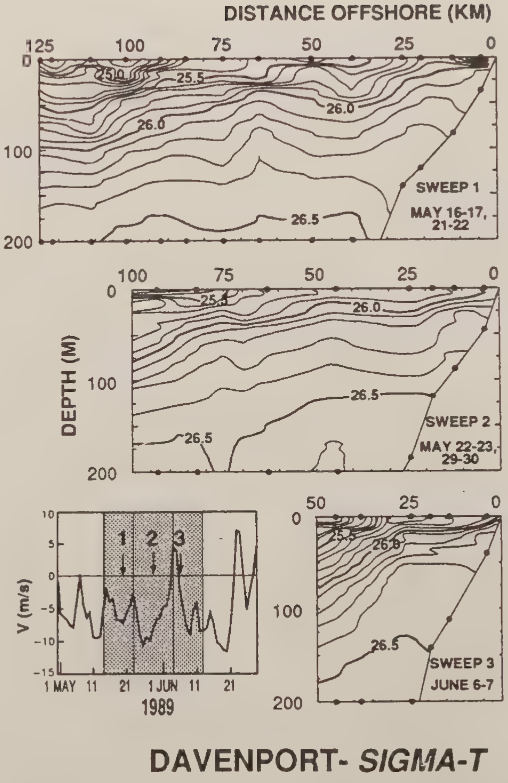

Figure 10. Vertical distribution of density along Davenport cross-shelf section (37°00′N), by sweep. Time series of the principal-axis wind component at NDBC buoy 46042 is included. *Bold arrows above the wind records* indicate the start of each survey.

Changes in the density structure off Davenport (figure 10) are representative of the temporal variability that existed during the survey period, and show the close relationship between ocean structure and coastal wind conditions. Wind during sweeps 1 and 2 was upwelling-favorable. The hydrographic structure appears similar during these sweeps as well.

Isopycnal doming near the coast, to depths as great as 100 m, defines the local upwelling center seen in the horizonal maps (figures 4–6) and AVHRR images (figure 9), and affirms the idea, based on the temperature-salinity relationship (figure 7), that water upwells from about 50 m to the surface. Doming off Davenport is confined to within 10–20 km of the coast (figure 10), consistent with estimates of the Rossby baroclinic radius of deformation based on these CTD data.

Between sweeps 1 and 2, all isopycnals to depths of at least 200 m, the maximum depth of the CTD casts, shoaled in response to increasing southward wind. The 26.0 isopycnal actually surfaced during sweep 2. Over the same interval, the outcropping of the 25.5 isopycnal moved from 35 km to 75 km offshore. The generally higher densities during sweep 2 indicate more recently upwelled water, in agreement with the stronger southward wind.

Possibly the most striking temporal variability is associated with the position, strength, and slope of the offshore front that separates less dense (warm, fresh) offshore water from denser (cool, salty) water nearer the coast. The front was located about 90 km offshore during sweep 1. Following the strong wind reversal at the onset of sweep 3, this front intensified, steepened, and moved to within about 35 km of the coast. The ocean response was rapid, within a few days of the wind reversal. Near-surface stratification also increased after the reversal (i.e., the mixed-layer depth decreased). The pattern of increased near-surface stratification during periods of weak wind was also noted elsewhere in the survey region.

It is thought that low wind speed results in reduced vertical mixing, which allows heat entering the ocean from the atmosphere to be trapped in a relatively thin surface layer. Reversals also bring warmer air into the region: the air temperature at NDBC buoy 46042, off Monterey, increased by 3°C during the reversal at the beginning of sweep 2 (figure 3). The large excursions in the position and strength of the offshore front, and the general change in the region's surface temperature are evident in the SST images (figure 9).

The position of the offshore front near the Gulf of the Farallones (figure 11) also moved between sweeps, suggesting that the relative contribution of upwelling varies on time scales of 10 days or less. However, the source of upwelled water over this portion of the shelf does not appear to be "local." Although isopycnal doming is again evident over the continental shelf break and slope (>50 km offshore), isopycnals are relatively flat over the shelf. No upwelling within a Rossby radius of the coast is apparent. Thus most of the upwelled water in the gulf is probably advected from the north, as implied from the near-surface hydrographic maps (figures 4 and 5) and satellite SST images (figure 9). Contrast this with the Davenport section (figure 10), where there is significant isopycnal tilting up to the coast.

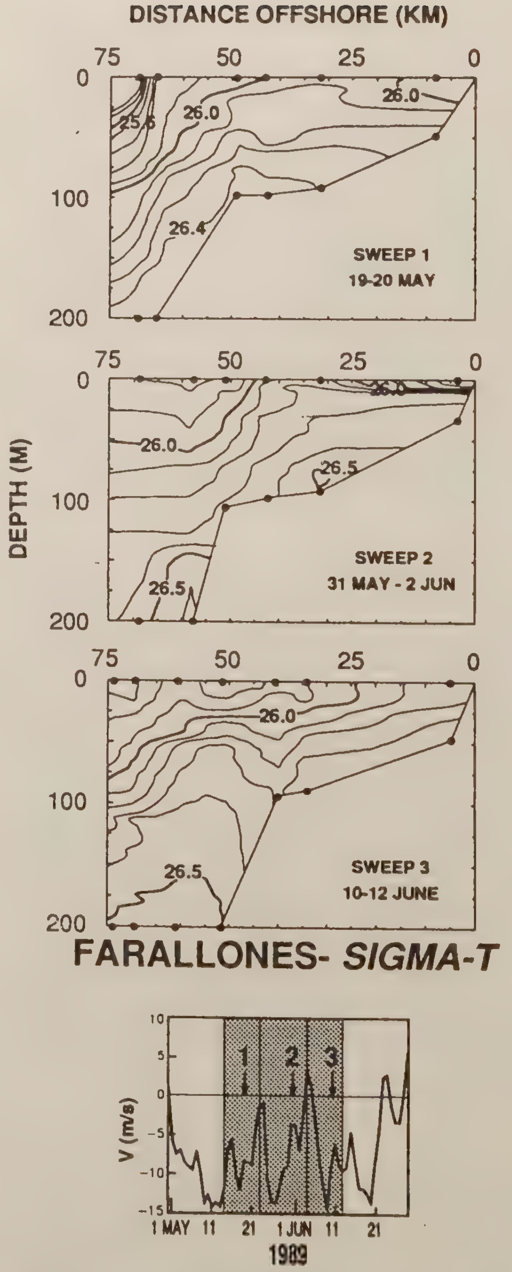

Figure 11. Vertical distribution of density along Farallones cross-shelf section (37°53′N), by sweep. Time series of the principal axis wind component at NDBC buoy 46026 is included. *Bold arrows above the wind records* indicate the start of each survey.

Although some of the isopycnal tilting over the slope off the Farallones may have been due to true upwelling, the structure is probably an artifact of the front that separates warm, fresh, offshore water from cool, saline, upwelled water. A density maximum is seen about 30–40 km offshore at this latitude, corresponding to the core of the cool water advecting south past Point Reyes. This mass of dense water appears even more distinct in contrast to the less-dense lens of water over the inner 20 km of the section, the source of which was probably San Francisco Bay outflow.

DISCUSSION

The hydrographic observations from the spring 1989 rockfish survey define a physical environment off central California that comprises several persistent and distinct water masses. The general locations of these masses are consistent throughout the 30-day survey period, and during the spring of other years as well (Schwing et al. 1990a). Most notable are two recently upwelled water masses off Point Reyes and Point Año Nuevo, which are separated from warmer and less saline offshore water by a distinct alongshelf front. Other distinct masses include the outflow from San Francisco Bay, and nearshore water, which is upwelled, advected onto the shallow portions of the shelf, and then warmed. Because much of this nearshore area is fairly sheltered from the wind, vertical mixing is reduced, and heat accumulates rapidly in the surface mixed layer. Nearshore areas also receive greater radiation because they are less susceptible to fog.

The location of each water mass, and of other circulation features described here, is linked to the physical processes characteristic of the site (e.g., wind forcing, flow/bathymetry interaction). The forces that contribute to the region's dynamics are the same everywhere; it is the *relative balance* of these forces — which varies (possibly greatly) with position — that leads to the seemingly incoherent arrangement of upwelling centers, fronts, and other dynamic features. For example, the proper combination of wind forcing and bathymetry is needed for upwelling to occur at a specific site. Given the rich environmental complexity off central California, it is not surprising that the coastal ocean displays such high mesoscale variability.

Despite their persistence, these water types vary substantially in extent and relative importance from sweep to sweep. Although wind direction during late spring is predominantly equatorward, or upwelling-favorable, the wind typically weakens or reverses direction at 3–10-day intervals (figures 2 and 3). The coastal ocean responds to such meteorological changes within 1–2 days. The strength of the offshore front that separates cool, salty shelf water from warmer, less saline offshore water seems directly linked to wind-relaxation events. Sharper fronts are observed immediately after relaxations or reversals of upwelling-favorable wind. The fronts also migrate closer to the coast after wind-relaxation events.

The dynamics behind this pattern may be relatively straightforward. During upwelling, an offshore flow in the surface Ekman layer sets up a cross-shelf pressure gradient and isopycnal doming within a Rossby radius of the coast. These gradients are balanced by an equatorward geostrophic current. Under steady upwelling conditions, the offshore surface flow is mass balanced by along-isopycnal flow toward the coast at depth. The resulting counterclockwise vertical cell (looking north) is confined inshore of the upwelling front.

A decrease or reversal in wind stress creates an unbalanced situation. An onshore flow develops to adjust the cross-shelf gradient. This flow is revealed by the rapid onshore movement of the offshore front. The circulation of the inshore cross-shelf cell is opposite the circulation during upwelling. Whereas the seasonal upwelling flow is controlled primarily by the density field, the 3–10-day variations in upwelling are largely barotropic (Mooers et al. 1978). Another effect of episodic upwelling periods separated by relaxation events is a long-term circulation that is a hybrid of these two regimes (Smith et al. 1971; Send et al. 1987). This highly complex residual circulation may maintain larvae and their prey near the highly productive upwelling centers. Direct velocity measurements are needed to confirm this conceptual model of the upwelling/relaxation circulation based on hydrographic and satellite data.

Our observations reveal that recently upwelled water flows offshore and equatorward as two distinct streamers separated by a warm, less saline water mass. Some unknown dynamic process exists that either (1) forces warm offshore meanders near the shelf or (2) forces separate upwelling streamers to the west and south, and causes the subsequent complex frontal interaction between these masses. We are examining this phenomenon in more detail. Some recent studies describing the behavior of filaments as they flow offshore, and in some cases retroflect (Strub et al. 1991) may shed light on this problem. The mechanism responsible for the variegated offshore front is also not known. Several possibilities exist: barotropic or baroclinic instabilities, spatial wind variability (wind curl), or variations in bathymetry.

Of particular interest to fisheries oceanographers is how the important coastal processes, water masses, and features off central California affect fisheries recruitment in the region. In the paragraphs below, we discuss some of the key physical processes associated with the rockfish survey results, and speculate on their biological implications. Larval and juvenile groundfish may take advantage of these oceanographic processes to enhance development, avoid predators, and position themselves for favorable settlement as preadults.

1. General transport patterns. Consider first the typical, persistent circulation of the region during spring. The mean flow generally parallels the near-surface isotherms, with cooler water on the left when looking downstream. The hydrographic structure in the upper 200 m implies a predominantly equatorward surface current over the entire region. Previous current-meter studies between the Farallones and Monterey Bay have measured predominantly southward velocities, typically 20–30 cm/s, during the upwelling season (Strub et al. 1987a; Chelton et al. 1988). Superimposed on this pattern are numerous eddylike features, whose horizontal scales are typically 10 km, that extend as deep as 100 m. The circulation is typically clockwise around a warm feature, and counterclockwise around a cool-water mass.

Species with long larval stages are likely to be transported a substantial distance southward by the mean flow. In the absence of any other transport mechanism or behavioral strategy that precludes long-distance transport, recruitment within a central California population will probably be provided by a stock to the north. Mesoscale features, which appear to be somewhat persistent, may be one mechanism for maintaining larvae near their source, or at least aggregating them before settlement. These features may also concentrate and enhance primary and secondary production, which could attract larvae and promote their development (Hayward and Mantyla 1990). Finally, the well-defined and persistent alongshelf front that separates offshore and shelf water may also separate areas of high and low biological productivity (Hood et al. 1990).

2. Discrete, persistent upwelling centers. Our observations suggest that upwelling does not occur uniformly along the central California coast, but is confined to several discrete upwelling centers. The dominant centers in this region appear to be somewhere north of Point Reyes, near Point Año Nuevo, and at Point Sur, to the south of the survey region. The three-dimensional structure of these centers is associated with variations in alongshelf and vertical flow, which are due to spatial differences in the wind field, bathymetric irregularities, and coastline irregularities (Smith 1983). Variable coastal upwelling and advection produces a complex hydrography and circulation near the coast, and numerous cross-shelf as well as alongshelf fronts. Thus certain locations along the coast associated with this variability may be more favorable for the aggregation and development of groundfish larvae and their prey. Closely spaced physical and biological sampling is required to properly resolve this complexity *in situ*.

Frequency of wind reversals. Wind forcing is not continuously upwelling-favorable in time, but relaxes or reverses direction every three to ten days. As our results demonstrate, an onshore surface flow develops in response to each relaxation event. This flow, which is evidenced by the rapid onshore movement of the offshore front, may also transport nutrient-rich water, plankton, and larval fish back toward the coast, or at least maintain their position fairly close to the coast. A poleward component of flow also develops during relaxation (Send et al. 1987) and may limit the extent that larvae are transported alongshore before settlement. At least, the absence of continuous upwelling precludes upwelled water and its contents from being transported far offshore, and into the southward-flowing California Current. Episodic upwelling regularly provides nutrients to the coastal environment while it maintains material, including larval and juvenile fish, relatively close to the source of high productivity.

4. Frontal position, strength, and variability. The offshore front moves rapidly onshore and strengthens during wind reversals. As it moves onshore, it probably transports and accumulates material in the frontal zone. Preliminary analysis suggests that the largest hydrographic variability in this region is along fronts (Schwing et al. 1990a). This variability probably is associated with the 3–10-day wind variability described in this paper. Evidence suggests that plankton biomass is maximized relative to offshore filaments (Abbott and Zion 1987; Hood et al. 1990). Larger organisms may be able to detect these variations and position themselves in productive frontal zones. Future analyses will correlate larval and juvenile abundance with frontal position, to test the hypothesis that fronts aggregate fish. Aggregation may be either active (fish are transported with the front) or passive (higher prey concentrations within the front attract larvae and juveniles).

5. Aging of upwelled water. Some time lag exists between the initial upwelling of nutrient-rich water, the peak in primary production, and the peak in secondary production. "Aged" upwelled water may be a more productive trophic environment for larval and juvenile groundfish. Episodic upwelling events bring pulses of productive water to the surface, where — under the right environmental conditions — energy is sequentially passed up trophic levels to the groundfish. Again the importance of the offshore front as a mechanism for concentrating nutrients and plankters is evident. If offshore flow is continuous or too strong, these materials will disperse rapidly, creating a relatively unproductive environment for larval growth. Another potentially productive environment is upwelled water trapped in cyclonic eddies (Hayward and Mantyla 1990).

It is still not known how, and to what degree, larval and juvenile groundfish respond to these physical factors to maintain a position that best helps them grow rapidly, avoid predators, and settle in optimal sites. The complexity of the region's physical oceanography is reflected in the temporal and spatial variability of phytoplankton (Hayward and Mantyla 1990; Hood et al. 1990) and zooplankton (Abbott and Zion 1987). This complexity may selectively fractionate biological organisms by size or taxonomic group as well (Hood et al. 1990). For example, a phytoplankter's position is totally controlled by the current regime, whereas zooplankton can modify their position with their behavior to abet or minimize their transport. Smaller groundfish larvae are much more at the mercy of the flow than are juveniles and preadults. Thus when considering how the processes and features of circulation affect a region's biological variability, the behavioral capabilities of the organism in question must be addressed specific to its life history and trophic level. One intriguing prospect is that dynamic features act as "trophic traps" for fish; i.e., eddies and fronts that concentrate plankton ultimately may attract fish, concentrating them as well.

We have provided a conceptual model of the spring circulation off central California, and speculated how it may directly and indirectly affect fish distribution and abundance. But there is still much to be learned about this coastal environment. This will require more detailed synoptic field measurements that combine physical and biological sampling; the development of refined process models; and, ultimately, coupled physical-biological models that realistically account for behavioral effects.

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LITERATURE CITED

Abbott, M. R., and P. M. Zion. 1987. Spatial and temporal variability of phytoplankton pigment off northern California during Coastal Ocean Dynamics experiment 1. J. Geophys. Res. 92:1,745–1,755.

Briggs, J. C. 1974. Marine zoogeography. McGraw-Hill, New York.

Chelton, D. B., R. L. Bernstein, A. Bratkovich, and P. M. Kosro. 1988. Poleward flow off central California during the spring and summer of 1981 and 1984. J. Geophys. Res. 93:10,604–10,620.

Gunderson, D. R., and T. M. Sample. 1980. Distribution and abundance of rockfish off Washington, Oregon, and California during 1977. Mar. Fish. Rev. 4:2–16.

Hayward, T. L., and A. Mantyla. 1990. Physical, chemical and biological structure of a coastal eddy near Cape Mendocino. J. Mar. Res. 48:825–850.

Hood, R. R., M. R. Abbott, A. Huyer, and P. M. Kosro. 1990. Surface patterns in temperature, flow, phytoplankton biomass and species composition in the Coastal Transition Zone off northern California. J. Geophys. Res. 95:18,081–18,094.

Horn, M. H., and L. G. Allen. 1978. A distributional analysis of California coastal marine fishes. J. Biogeogr. 5:23–42.

Huyer, A., E. J. Sobey, and R. L. Smith. 1979. The spring transition in currents over the Oregon shelf. J. Geophys. Res. 84:6,995–7,011.

Lentz, S. J. 1987. A description of the 1981 and 1982 spring transitions over the northern California shelf. J. Geophys. Res. 92:1,545–1,567.

McClain, E. P., W. G. Pichel, and C. C. Walton. 1985. Comparative performance of AVHRR-based multichannel sea surface temperatures. J. Geophys. Res. 90:11,587–11,601.

Mooers, C. N. K., C. N. Flagg, and W. C. Boicourt. 1978. Prograde and retrograde fronts. *In* Oceanic fronts in coastal processes, M. J. Bowman and W. E. Esaias, eds. Berlin: Springer-Verlag. pp. 43–58.

Murray, S. N., M. M. Littler, and I. A. Abbott. 1980. Biogeography of the California marine algae with emphasis on the southern California islands. *In* The California islands, D. M. Power, ed. Santa Barbara: Santa Barbara Museum of Natural History. pp. 325–339.

PFMC (Pacific Fishery Management Council). 1989. Status of the Pacific Coast groundfish fishery through 1989 and recommended acceptable biological catches for 1990. Pacific Fishery Management Council, Portland, Ore. 49 pp. + appendices.

Schwing F. B., D. M. Husby, D. E. Tracy, S. V. Ralston, and W. H. Lenarz. 1990a. Hydrographic conditions in the Gulf of the Farallones following the spring transition. Trans. Am. Geophys. Union. 71:1,350.

Schwing F. B., S. Ralston, D. M. Husby, and W. H. Lenarz. 1990b. The nearshore physical oceanography off the central California coast during May–June, 1989: a summary of CTD data from juvenile rockfish surveys. U. S. Depart. Commerce, NOAA Tech. Memo. NOAA-TM-NMFS-SWFC-153, 10 pp. + appendices.

Send, U., R. C. Beardsley, and C. D. Winant. 1987. Relaxation from upwelling in the Coastal Ocean Dynamics Experiment. J. Geophys. Res. 92:1,683–1,698.

Smith, R. L. 1983. Circulation patterns in upwelling regimes. *In* Coastal upwelling, Pt. A, E. Suess and J. Thiede, eds. New York: Plenum Publishing, pp. 13–35.

Smith, R. L., C. N. K. Mooers, and D. B. Enfield. 1971. Mesoscale studies of the physical oceanography in two coastal upwelling regions: Oregon and Peru. *In* Fertility of the sea, vol. 2, J. D. Costlow, Jr., ed. New York: Gordon and Breach, pp. 513–535.

Strub, P. T., J. S. Allen, A. Huyer, R. L. Smith, and R. C. Beardsley. 1987a. Seasonal cycles of currents, temperatures, winds, and sea level over the northeast Pacific continental shelf: 35°N to 48°N. J. Geophys. Res. 92:1,507–1,526.

Strub, P. T., J. S. Allen, A. Huyer, and R. L. Smith. 1987b. Large-scale structure of the spring transition in the coastal ocean off western North America. J. Geophys. Res. 92:1,527–1,544.

Strub, P. T., and the CTZ Group. 1991. The nature of the cold filaments in the CCS. J. Geophys. Res. 96:14,743–14,768.

Tracy, D. E. 1990. Source of cold water in Monterey Bay observed by AVHRR satellite imagery. M.S. thesis. Naval Postgraduate School, Monterey, Calif.

Valentine, J. W. 1966. Numerical analysis of marine molluscan ranges on the extratropical northeastern Pacific shelf. Limnol. Oceanogr. 11:198–211.

Wyllie-Echeverria, T., W. H. Lenarz, and C. A. Reilly. 1990. Survey of the abundance and distribution of pelagic young-of-the-year rockfishes off central California. U.S. Depart. Commerce, NOAA Tech. Memo. NOAA-TM-NMFS-SWFC-147, 125 pp.

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Some Notes on the Early Life Stages of the Pacific Pomfret, *Brama japonica*, and Other Bramidae from the Central North Pacific Ocean

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Fishes of the percoid family Bramidae are widespread, occurring in all tropical and temperate seas but, with the exception of the two most abundant species of the genus *Brama*, are poorly studied (Mead, 1972). The biology of the family is best known in the Atlantic Ocean and much less so in the Pacific. In particular, information is limited regarding the reproduction and early life history of North Pacific bramids. For many years, nearly all knowledge on Pacific bramids was contained in Mead's impressive 1972 monograph. Since then, Kinoshita (1988) has presented larval descriptions of western North Pacific bramids, a new genus and species from the South Pacific have been described (Yatsu and Nakamura, 1989), and a few studies have been conducted on the biology and distribution of *Brama japonica* (Pacific pomfret, shimagatsuo), a major species taken in the North Pacific drift-net fisheries (Shimazaki, 1989).

Knowledge of the biology of *B. japonica* has grown considerably with the expansion of the commercial salmon and squid drift-net fisheries across the North Pacific Ocean. Although pomfret are not the target of these fisheries, the substantial number of *B. japonica* taken incidentally has stimulated increased interest in and research on the resource. Studies of pomfret distribution based upon drift-net catch data (Neave and Hanavan, 1960; Hitz and French, 1965; Machidori and Nakamura, 1971) provided the basis for the seasonal migration patterns suggested by Shimazaki and Nakamura (1981) (Fig. 1). Briefly adult *B. japonica* are known to occupy feeding grounds in North Pacific subarctic waters above 40°N latitude during the summer months. The species is then hypothesized to migrate south to subtropical spawning areas within the North Pacific Transition Zone between 20°N and 40°N latitude. Based upon gonadosomatic index (GSI) values, Yoon and Shimazaki (1981) predicted *B. japonica* to

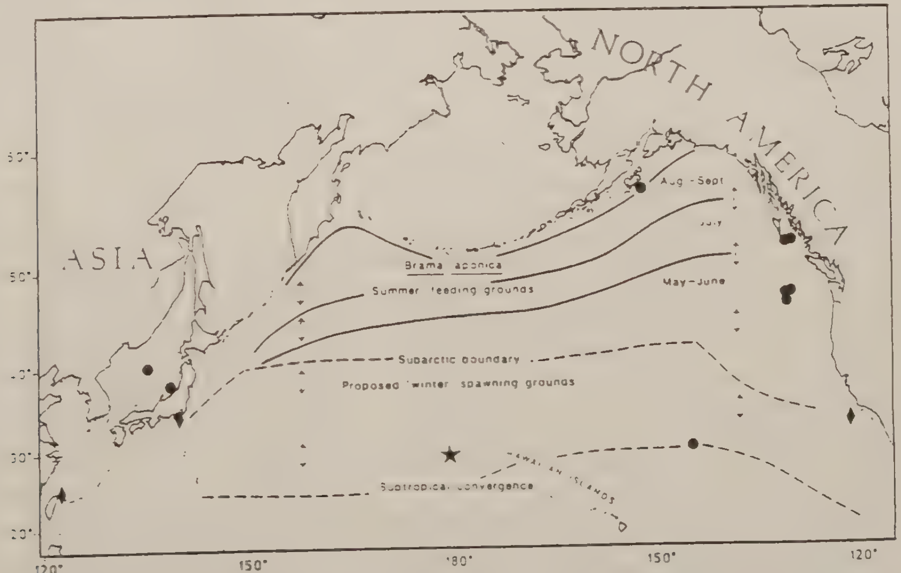

Fig. 1. Distribution of *Brama japonica* and *Taractes asper* in the North Pacific. The asterisk indicates the Southeast Hancock Seamount (29°47′N, 179°03′E), where early stages of four bramid species were collected. Circles indicate *T. asper* 200 mm SL; diamonds indicate *T. asper* 200 mm SL. The seasonal distribution of *B. japonica* (adapted from Shimazaki and Nakamura, 1981) is indicated by solid and broken lines.

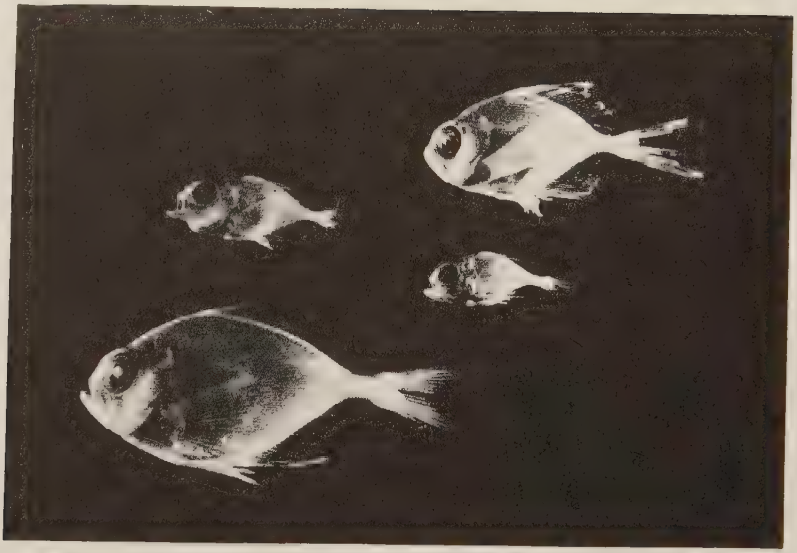

Fig. 2. Juvenile *Brama japonica* from the Southeast Hancock Seamount: 15.1, 19.5, 26.0, and 38.6 mm

be protracted multiple spawners during the winter months of December-April and from early June-July. Wada and Murata (1985) also reported that GSI values tend to be lowest in August and to rapidly rise during October-November.

In this note, we discuss collections that provide new insight into bramid reproduction and distribution in the central North Pacific Ocean.

Materials and methods

Micronekton and plankton samples were collected at the Southeast (SE) Hancock Seamount (29°47′N, 179°03′E). Micronekton samples were collected with a 1.8 m Isaacs-Kidd midwater trawl (IKMT) (February 1985, November 1986, April 1987, January 1988, July-August 1988, and October 1988), a 60 m^2 Marinovich trawl (September and November 1986), and a 100 m^2 Oregon State University (OSU) rope trawl (November 1988). Bramid eggs and larvae were collected in plankton samples using a 1 m^2 opening-closing Tucker trawl (July 1984 and February 1985), a 0.49 m^2 Manta (neuston) net (January 1988), and a 60 cm bongo net (January 1988). To determine whether the densities of larvae at the seamount and in the surrounding ocean differed, paired sets of samples were taken directly above the seamount summit and at stations 20 km to the west of the summit in July 1984 and February 1985.

All samples were preserved in 10% form
and sorted for bramid larvae and juveni
laboratory. Bramid eggs were removed
samples taken in January 1988, but eggs
routinely sorted from the samples. Specir
identified by the criteria of Mead (1972)
shita (1988). They were also compared
ern Pacific specimens of *B. japonica* from
fornia Cooperative Oceanic Fisheries Inv
(CALCOFI).

Results and discussion

Brama japonica, Pacific pomfret, shima

Our collections of large larvae and juver
japonica at SE Hancock Seamount suppo
pothesis of Shimazaki and Nakamura (1981
subtropic region is indeed a winter spawnin
the Pacific pomfret. Thirteen larval and j
japonica (Fig. 2), 8.1–38.6 mm standard len
were collected over and near the seamount
horizontal and oblique IKMT tows at
≤250 m (usually 75–135 m; Table 1). All
the young pomfret were collected in Febr
and January 1988, although sampling was
in all months except March, May, and
IKMT tows in January-February, 14 in A
July-August, and 33 in October-Novem

single 32.5 mm SL specimen was collected in April 1987.

Collections of 11 bramid eggs and 62 larvae from plankton samples taken near the seamount in February 1985 and January 1988 (Tables 2, 3) also support the hypothesis of winter spawning of *B.*

Table 1. Collection data for *Brama japonica* in 1.8 m Isaacs-Kidd midwater trawl tows at the Southeast Hancock Seamount. S = captured on seamount summit; W = captured 20 km west of the seamount summit.

SL (mm)	Date	Start time	Tow duration (min)	Max. depth fished (m)	Location
8.1	16 Jan. 1988	2321	67	110	S
9.0	12 Feb. 1985	2114	62	72	W
9.4	12 Feb. 1985	0555	46	117	S
9.6	12 Feb. 1985	2258	57	135	W
10.6	12 Feb. 1985	2114	62	72	W
11.2	16 Jan. 1988	2321	67	110	S
13.9	12 Feb. 1985	2114	62	72	W
15.1	13 Feb. 1985	0612	46	119	W
19.5	13 Feb. 1985	0612	46	119	W
26.0	13 Feb. 1985	0612	46	119	W
28.5	28 Jan. 1988	2304	69	250	S
32.5	19 Apr. 1987	2155	56	200	S
38.6	28 Jan. 1988	2115	69	250	S

Table 2. Collection data for *Brama japonica* captured with a 1 m^2 Tucker trawl at the Southeast Hancock Seamount in February 1985. D = day sample; N = night sample. Except where noted otherwise, data were from a series of paired samples taken to compare the occurrence of larvae over and away from the seamount during day and night. Eight tows at depths of 100–200 m were excluded, because no *Brama* were collected.

D/N	Depth (m)	20 km west of the seamount				Above the seamount summit			
		Date	Start time	Larvae/ 1000 m^3	SL (mm)	Date	Start time	Larvae/ 1000 m^3	SL (mm)
D	0– 25	4	0916	2.61	4.2–5.9	9	0848	2.33	3.8– 3.9
D	0– 25	4	1145	1.10	10.0	9	1046	2.35	3.2– 3.9
D	25– 50	4	0859	0		9	0830	2.27	4.9– 9.9
D	25– 50	4	1122	0		9	1028	2.19	10.5–11.2
D	50–100	4	1022	2.06	4.0–5.9	9	0932	0	
D	50–100	4	1354	0		9	1346	1.09	3.7
D	0– 50	4	1045	0		9	0950	2.31	2.8– 3.8
D	0– 50	4	1416	1.20	3.6	9	1404	1.12	4.4
D	0–100	4	1315	0		9	1248	2.21	4.3– 8.4
D	0–100	4	1530	0		9	1515	0	
N	0– 25	8	2032	0		9	2030	0	
N	0– 25	8	2224	1.07	3.6	9	2235	0	
N	25– 50	8	2011	3.11	3.4–6.0	9	2012	5.36	3.3– 6.6
N	25– 50	8	2207	2.12	3.6–3.6	9	2217	1.15	3.8
N	50–100	8	2106	1.12	2.9	9	2113	2.13	3.9–10.5
N	50–100	9	0010	1.15	8.1	10	0038	0	
N	0– 50	8	2125	2.19	3.9–7.0	9	2145	0	
N	0– 50	9	0030	0		10	0100	0	
N	0–100	8	2330	0		10	0000	0	
N	0–100	9	0145	0		10	0215	0	
D[1]	0– 50	23	0047	4.71	3.0–9.7				
D[1]	0–100	23	0012	1.24	3.9				

[1] Data are from other sample series not completely sorted for bramid larvae.

japonica in this region. No *Brama* larvae were collected in 51 plankton samples in July 1984.

We suggest that most of the eggs and larvae collected during the winter were *B. japonica*, based on known adult distributions and the proportions of juveniles in our collections. Nine large (7.0–11.2 mm SL) larvae were identified as *B. japonica* with certainty. The eggs and smaller larvae lacking fin rays could not be unequivocally identified, but myomere counts (36–42; 73% with 38–39; one each with 36 and 42) indicate that they are *B. japonica*, *B. orcini*, or *Taractes asper*. A single adult *B. orcini*, which has a tropical distribution in >18.3℃ water opposing the temperate distribution of *B. japonica* (Mead, 1972), reportedly was caught at the seamount during summer (Humphreys et al., 1984). Sea surface temperatures at the seamount were 16.5°–18.4℃ in February 1985 and 17.8°–19.4℃ in January 1988.

Bramid larvae collected with opening-closing nets were all taken at depths of 0–100 m, with none in eight tows at 100–200 m and most at 0–50 m (Table 2). The vertical distribution of the larvae indicates that they occur throughout the mixed layer (0–90 m as determined from XBT casts) without evidence of diel migration. This mixed layer distribution is further supported by the capture of most juveniles from the IKMT in tows at <120 m (Table 1).

Catches of *Brama* larvae during February 1985 over the seamount summit were not significantly different from catches 20 km to the west (Wilcoxon paired-sample test, P>0.05; Table 2). Bramids thus probably spawn throughout the area and not specifically at seamounts, as demonstrated by larvae and juveniles captured in this region far from any shallow topographic feature (Mead, 1972; Loeb, 1979a, b).

Historically, winter spawning of *B. japonica* in this region is supported by the capture of 10 larvae at 31°–33°N, 166°–174°W in March-May 1933 (Mead, 1972). Loeb (1979a, b) reported the capture of 52 larval *B. japonica* near 28°N, 155°W. Unfortunately, except for three individuals collected in September 1968 (Loeb, 1979b), no information on seasonality of capture has been presented. During ichthyoplankton surveys conducted by the CALCOFI cruises, bramid larvae (primarily *B. japonica*; H. G. Moser, personal communication, May 1990) were collected throughout the year in the eastern North Pacific off California, with peak numbers of larvae captured in January, July, and October (see Ambrose et al. (1988) data references). Although our IKMT sampling also was conducted during summer in 1984, 1987, and 1988, we have no evidence of the hypothesized June-July spawning period. This may reflect that pomfret occupying waters toward the eastern Pacific (i.e. west longitudes) spawn later in the year than their western counterparts. Adult pomfret captured around 35°–45°N, 140°–175°W had high GSI values in June-July and completed spawning in late July, but fish sampled to the west at 30°–40°N, 160°–170°E had GSI values indicating the end of spawning in May (Yoon and Shimazaki, 1981).

Taractes asper, rough pomfret, manzai-uo

Three juvenile *T. asper*, 14.5, 15.8, and 20.5 mm

Table 3. Collection data from positive tows for *Brama japonica* captured above the summit of the Southeast Hancock Seamount with a 60 cm bongo net and 0.49 m² neuston net during January 1988. Bramids were absent in 16 other bongo net and 3 other neuston samples. No samples were collected away from the summit during this cruise. Bramid eggs were not identified from most samples.

Date	Start time	Depth (m)	Number of larvae	SL (mm)
14	Night (0115)	0–1	3	3.0–4.5
14	Night (0540)	0–100	6	3.3–5.9, 4 eggs
14	Night (2015)	0–1	2	3.5–3.8
14	Night (2254)	0–1	4	2.6–3.8
15	Night (0247)	0–1	3	4.2–4.8
15	Night (0508)	0–1	2	3.6–3.7
17	Night (2036)	0–50	4	3.1–3.5, 3 eggs
15	Night (0009)	0–100	1	3.8
15	Night (0356)	0–100	2	3.1–4.5, 3 eggs
15	Night (0605)	0–100	3	3.4–5.1
15	Night (2008)	0–100	3	3.2–5.2, 1 egg
18	Night (0503)	0–100	1	3.6

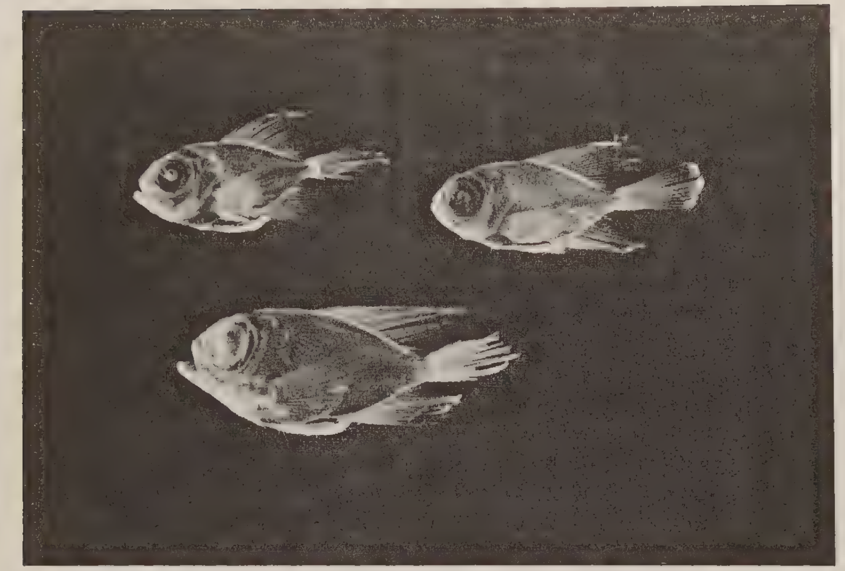

Fig. 3. Juvenile *Taractes asper* from the Southeast Hancock Seamount: 14.5, 15.8, and 20.5 mm SL.

SL (Fig. 3), were collected 20 km west of the SE Hancock Seamount summit in February 1985, 0612–0658 h, in a horizontal 1.8 m IKMT tow at about 119 m depth. This is the first record of the species from a specific locality in the central North Pacific, extending the known range of the species by about 3900 km. Borets and Sokolovskij (1978) included *T. asper* in the ichthyoplankton collected from the northern Hawaiian Ridge and the Emperor Seamounts but did not report capture locations.

Historically, very few occurrences of *T. asper* have been reported in the North Pacific (Fig. 1). Except for two large specimens taken at 30°N, 145°W (Mead, 1972—not shown on distribution map in monograph), *T. asper* previously have been reported in the North Pacific from only the continental shelf and slope waters of Asia and North America. Since Mead (1972), records include only a large 373 mm SL individual taken off the Queen Charlotte Islands (Peden and Ostermann, 1980), nine adults (291–392 mm SL) caught off the west coast of British Columbia (Peden and Jamieson, 1988), a 258 mm SL adult from the southern coast of Hokkaido, Japan (Amaoka et al., 1989), a 169 mm SL specimen off California (Pavlov, 1989), and, most recently, five adults from the shelf off southern Oregon (OSU cat. no. 6588).

The February capture supports speculation that, like *B. japonica*, *T. asper* may also be a subtropical winter spawner (Mead, 1972; Kinoshita, 1988).

Pterycombus petersii, prickly fanfish, ryûgû-no-hime

Because records of juvenile *Pterycombus petersii* from this region are virtually nonexistent, also noted here is the capture of a small (26.1 mm SL) individual with a 60 m^2 Marinovich herring trawl in November 1986.

Pteraclis aesticola, Pacific fanfish, benten-uo

Twenty-four larval and juvenile *Pteraclis aesticola* (2.3 to 47.2 mm SL) were collected during July-November. Larvae were only collected in July 1984, suggesting that this species spawns during the summer in this region.

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Literature cited

Amaoka, K., K. Nakaya and M. Yabe. 1989. Fishes of Usujiri and adjacent waters in southern Hokkaido, Japan. Bull. Fac. Fish. Hokkaido Univ., 40(4): 254–277.

Ambrose, D. A., R. L. Charter, H. G. Moser and B. S. Earhart. 1988. Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1981. NOAA Tech. Memo. NMFS-SWFC-112, 170 pp.

Borets, L. A. and A. S. Sokolovskij. 1978. Species composition of the ichthyoplankton of the Hawaiian submarine ridge and the Emperor Seamounts. Pages 43–50 *in* Izvestiya of the Pacific Ocean Scientific Research Institute for Fisheries and Oceanography (TINRO). Fisheries oceanography, hydrobiology, biology of fishes and other denizens of the Pacific Ocean. Vol. 102. (English translation by W. G. Van Campen for the Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Transl. No. 105, 10 pp.)

Hitz, C. R. and R. R. French. 1965. Occurrence of pomfret (*Brama japonica*) in the northeastern Pacific Ocean. Fish. Indust. Res. 3: 1–7.

Humphreys, R. L., Jr., D. T. Tagami and M. P. Seki. 1984. Seamount fishery resources within the southern Emperor-northern Hawaiian Ridge area. Pages 226–236 *in* R. W. Grigg and K. Y. Tanoue, eds. Proceedings of the Second Symposium on Resource Investigations in the Northwestern Hawaiian Islands, May 25–27, 1983, University of Hawaii, Honolulu, Hawaii. Vol. 2. UNIHI-SEAGRANT-MR-84-01.

Kinoshita, I. 1988. Bramidae. Pages 487–496 *in* M. Okiyama, ed. An atlas of the early stage fishes in Japan. Tokai Univ. Press, Tokyo. (English translation by W. G. Van Campen for the Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Transl. No. 130, 25 pp.)

Loeb, V. J. 1979a. Larval fishes in the zooplankton community of the North Pacific central gyre. Mar. Biol., 53: 173–191.

Loeb, V. J. 1979b. Vertical distribution and development of larval fishes in the North Pacific central gyre during summer. Fish. Bull., U.S., 77: 777–793.

Machidori, S. and S. Nakamura. 1971. Distribution and some biological informations of pomfret (*Brama raii*) in the northwestern North Pacific Ocean. Bull. Far. Seas Fish. Res. Lab., (5): 131–145.

Mead, G. W. 1972. Bramidae. Dana Rep., (81): 166 pp.

Neave, F. and M. G. Hanavan. 1960. Seasonal distribution of some epipelagic fishes in the Gulf of Alaska region. J. Fish. Res. Bd. Can. 17: 221–233.

Pavlov, Y. P. 1989. Some data on the morphometrics and distribution of species of the genus *Taractes* (Bramidae) in the Pacific Ocean. Voprosy Ikhtiologii, (4): 660–662. (English translation in J. Ichthyol., 29: 164–166.)

Peden, A. E. and G. S. Jamieson. 1988. New distributional records of marine fishes off Washington, British Columbia and Alaska. Can. Field. Nat., 102: 491–494.

Peden, A. E. and W. Ostermann. 1980. Three fish species previously unknown from marine waters off British Columbia. Syesis, 13: 215–217.

Shimazaki, K. 1989. Ecological studies of the pomfret (*Brama japonica*) in the North Pacific Ocean. Pages 195–205 *in* R. J. Beamish and G. A. McFarlane eds. Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models. Can. Spec. Publ. Fish. Aquat. Sci., 108.

Shimazaki, K. and S. Nakamura. 1981. Ecological studies of the pomfret (*Brama japonica* Hilgendorf). I. The seasonal distributional pattern and ecological considerations. Res. Inst. North Pac. Fish., Hokkaido Univ., Special Vol.: 91–103. (In Japanese with English abstract.)

Wada, T. and M. Murata. 1985. Distribution and biological characteristics of pomfret, *Brama japonica* Hilgendorf, in the Pacific Ocean off northern Japan. Bull. Hokkaido Reg. Fish. Res. Lab., (50): 1–12.

Yatsu, A. and I. Nakamura. 1989. *Xenobrama microlepis*, a new genus and species of bramid fish, from subantarctic waters of the South Pacific. Japan. J. Ichthyol., 36(2): 190–195.

Yoon, T. H. and K. Shimazaki. 1981. Ovarian maturation of the Pacific pomfret, *Brama japonica* Hilgendorf, in the North Pacific Ocean. Res. Inst. North Pac. Fish., Hokkaido Univ., Special Vol.: 79–90. (In Japanese with English abstract.)

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北太平洋中部から採集されたシマガツオ科の仔稚魚

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北太平洋の Southeast Hancock Seamount から，シマガツオ科のシマガツオ，マンサイウオ，ヘンテンウオの3種の卵，仔稚魚を採集した．採集データに基づき，これらの産卵期，分布などを論議した．

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Ultrastructure of the epidermis and digestive tract in *Sebastes* embryos, with special reference to the uptake of exogenous nutrients

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Key words: Viviparity, Nutrition, Horseradish peroxidase, Ruthenium red, Pinocytosis, Rockfish, Pisces, Scorpaenidae

Synopsis

Ultrastructural features of the epidermis and rectum were studied in *Sebastes schlegeli* and *S. melanops* during the late stages of embryonic development, to confirm uptake of maternal substances. Ruthenium red (RR) and horseradish peroxidase (HRP) were used at fixation and in live embryos, respectively. Epidermal tissue of embryos after developmental stage 24 comprised two squamous cell layers. The outer, thinner cells and their intercellular spaces were easily infiltrated with RR, but the inner cells had no RR deposition. The HRP was not incorporated into the epidermis except in a few outer cells, which had well-developed microvillous projections of cytoplasm. Sacciform cells, chloride cells, and mucous cells distributed in the inner layer but protruding to the epidermal surface had no intracellular RR and HRP depositions. The rectal cells of embryos at about developmental stage 28 had many globular inclusions containing electron-dense substances. The rectal cells were found to take up and digest HRP actively. It is suggested that the embryonic epidermis is structurally loose and takes up low weight molecules, while rectal cells, after the opening of the mouth, actively ingest exogenous, high weight molecules.

Introduction

In larvae of many oviparous fishes, the hindgut has a unique feature for pinocytotic ingestion and intercellular digestion of high molecular weight nutrients (Iwai 1969, Tanaka 1969, Watanabe 1982). Embryos of many viviparous teleosts possess specific organs, such as the trophotaenia and the vasculated finfold, adapted for the uptake of nutrients from the maternal ovarian fluid (Turner 1947, Mendoza 1958, Wourms et al. 1988). Absorption of external nutrients through the embryonic epidermis has been reported in two viviparous species, *Goodea luitpoldii* and *Clinus superciliosus* (Mendoza 1958, Veith 1979, 1980).

The scorpaenid genus *Sebastes* has been categorized as ovoviviparous, because the internal embryos were considered to be lecithotrophic with no specific organs for taking up external nutrients. Recent studies on energetics, however, suggest that embryos of *S. schlegeli* and *S. melanops* utilize external materials as energy sources (Boehlert &

Yoklavich 1984, Boehlert et al. 1986). Those studies also present indirect histological evidence that the rectal cells of *Sebastes* embryos at late developing stages may function in the ingestion of exogenous substances, but offer no direct evidence of the absorption of nutrients by either rectal epithelial or epidermal cells.

Our paper presents direct ultrastructural evidence that the epidermis and the rectum in *Sebastes* embryos absorb external substances, using horseradish peroxidase (HRP) and ruthenium red (RR) as tracers.

Materials and methods

Intraovarian embryos and just hatched larvae of *Sebastes schlegeli* and *S. melanops* were used. Determinations of the developmental stages of the embryos followed Yamada & Kusakari (1991). Embryos before stage 32 were obtained by catheterization through the genital pore of maternal fish. For the experiments using HRP, live embryos of *S. melanops* were incubated for 1–4 h in physiological saline (230 mM NaCl, 8 mM KCl, 2.3 mM $CaCl_2$, 3.7 mM $MgCl_2$ and 2.4 mM $NaHCO_3$, pH 7.3) containing 0.5% HRP and then rinsed in saline for 5 min. The embryos were fixed in toto with Karnovsky's (1965) fixative and, after being washed with 0.1 M sodium cacodylate buffer (pH 7.4) were treated for 15 min with 0.05% diaminobenzidine tetrahydrochloride (DAB) in 0.1 M Tris-HCl buffer (pH 7.4) containing 0.01% H_2O_2 and 0.5% sucrose. After they were washed with the buffer, they were post-fixed with 1% osmium tetroxide, dehydrated through a graded series of ethanol and embedded in Epok 812. For the other experiments, embryos were fixed with Karnovsky's (1965) fixative containing RR (1 mg ml^{-1}), osmicated with osmic solution containing RR and embedded in Epok 812.

The epidermal and rectal tissues were cut into ultrathin sections, which were then stained with uranyl acetate and lead citrate and examined with a Hitachi H-6000 transmission electron microscope (TEM). Some of the specimens treated with HRP were examined by light microscopy. For scanning electron microscopy (SEM), some fixed embryos were dehydrated through ethanol and isoamyl acetate and dried by the critical point method using liquid CO_2. After being coated with a thin layer of evaporated platinum-palladium alloy, they were examined with a JEOL JSM-25 scanning electron microscope.

Results

Epidermis

Sebastes embryos during the late developmental stages had thin, delicate skin composed of epidermal and dermal tissues over the main body surface and only epidermal tissue over the finfold. The epidermis comprised of two squamous cell layers: an outer layer (0.5–3 μm thick) with thin cells and an inner layer with thick cells and other types of cells such as sacciform, chloride and mucous cells. The apico-lateral membranes of the outer epidermal cells were connected with tight junctions and desmosomes. Embryos treated with RR had particles of RR deposited in the outer layer of the epidermis (Fig. 1a), particularly at the intercellular spaces and interdigitating infoldings. Infoldings dotted with RR particles were commonly seen in the lateral and basal membranes of the outer layer cells (Fig. 1b). Small vesicles dotted with RR were distributed in the apical zone (Fig. 1b, c), which was characterized by an abundance of cytoplasmic filaments. Some vesicles were in direct contact with the apical membrane. The RR particles were deposited also in the intracellular membranous systems, cisternae of the endoplasmic reticulum (ER) and mitochondria (Fig. 1c). Numerous RR-dotted cisternae of ER were distributed in the middle zone of the cell, where expanded mitochondria also were present. The RR particles were found in the perinuclear space as well (Fig. 1d).

Squamous cells of the inner epidermal layer, as compared with the outer layer cells, had well-developed rough-ER and abundant free ribosomes in the relatively compact cytoplasm (Fig. 1d). The apical membranes of these cells interdigitated with the basal membranes of the outer cells. No RR

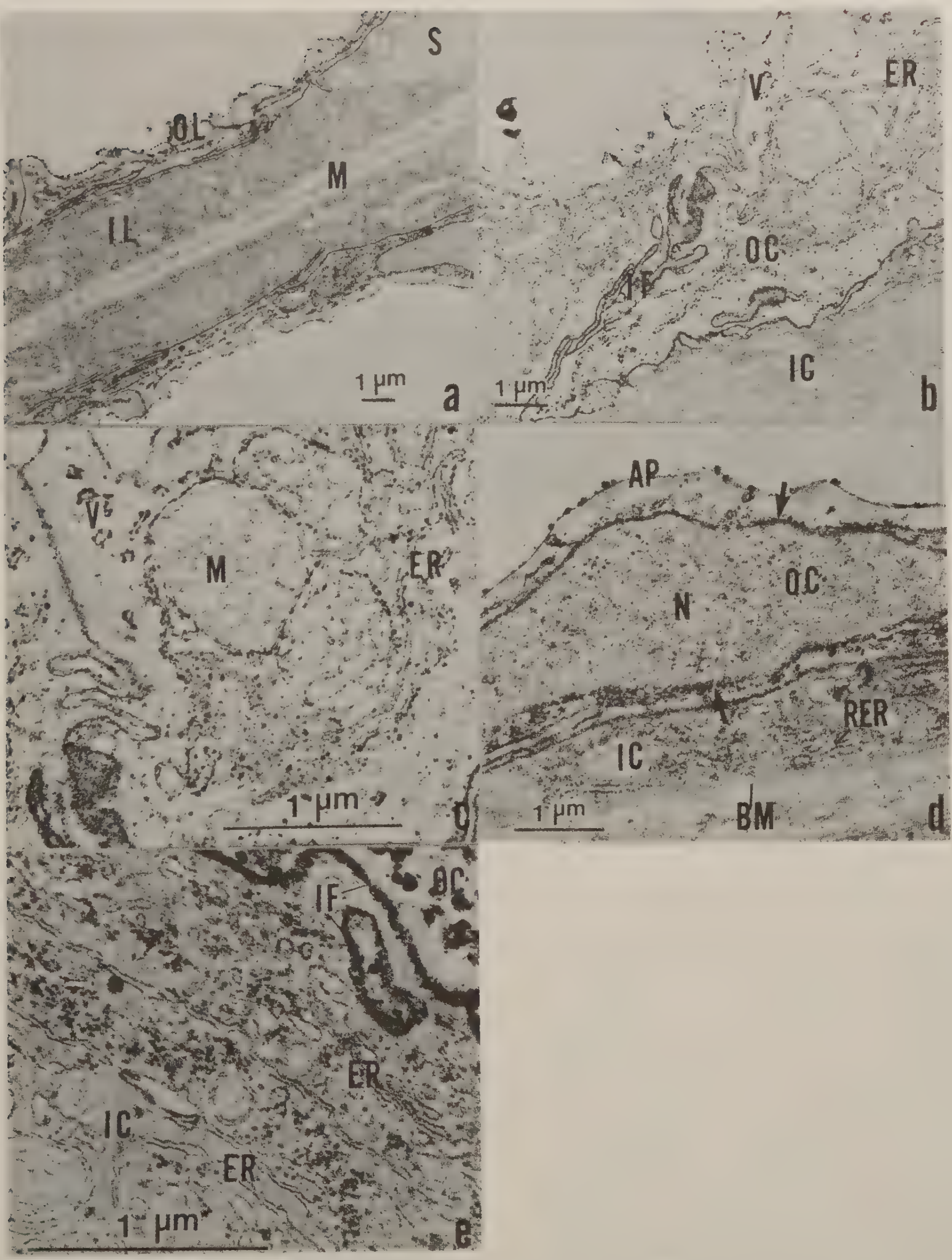

Fig. 1. Transmission electron micrographs of embryonic epidermal tissues, stained with ruthenium red, from *Sebastes melanops* at developmental stage 24: a – Transverse section of the finfold. IL = inner layer, OL = outer layer, M = muscle layer and S = sacciform cell. b – Interdigitations of the outer cells (OC) forming infoldings (IF) at the lateral and basal membranes. Arrows indicate vesicles attaching apical surface. V = vesicles, ER = endoplasmic reticulum and IC = inner cell. c – Membrane systems of endoplasmic reticulum (ER) and mitochondria (M). V = vesicles. d – Perinuclear space (arrows) in the outer cell (OC). AP = apical surface, BM = basement membrane, IC = inner cell, N = nucleus and RER = rough endoplasmic reticulum (ER). e – Inner cell (IC) interdigitating with an outer cell (OC). ER = endoplasmic reticulum, IF = infolding.

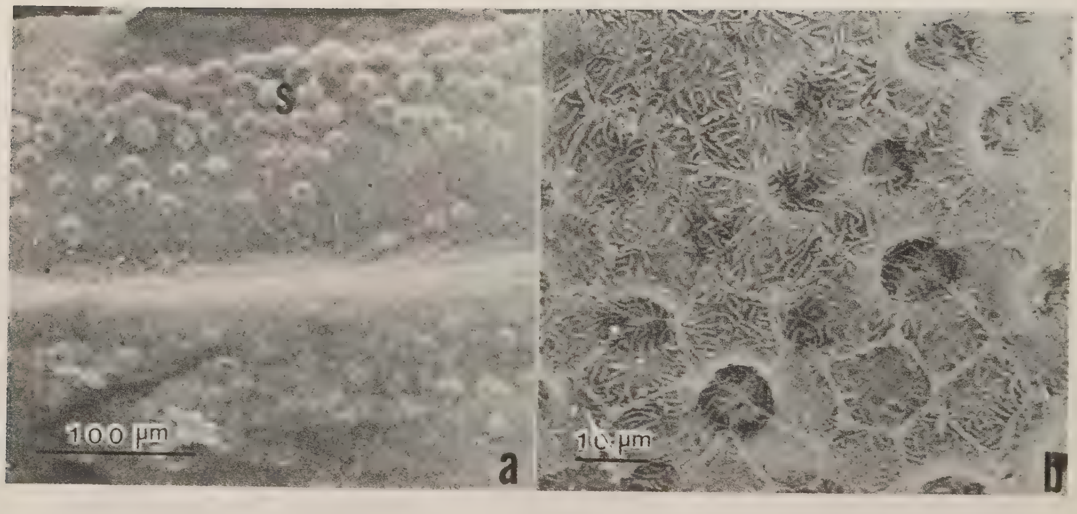

Fig. 2. Scanning electron micrographs of *Sebastes melanops* embryos: a – Swollen sacciform cells in the dorsal finfold (stage 28). b – Numerous depressions formed by shrunken sacciform cells in the jaw region (stage 28).

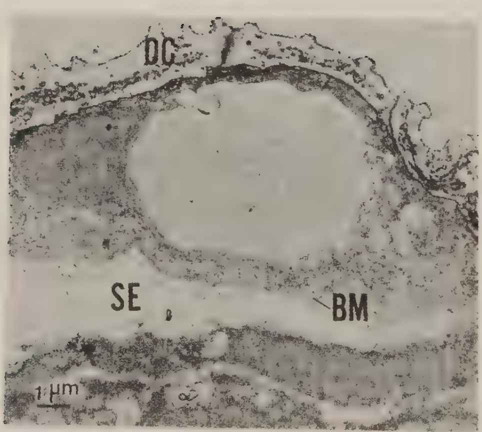

Fig. 3. Transmission electron micrograph of a swollen sacciform cell in a *Sebastes melanops* embryo at stage 24, stained with ruthenium red. BM = basement membrane, OC = outer cell and SE = subepidermal space.

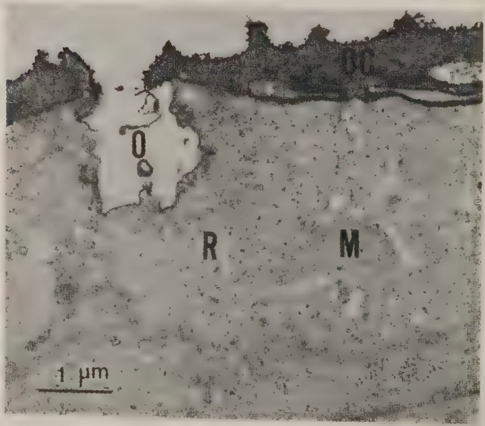

Fig. 4. Transmission electron micrograph of a chloride cell in a *Sebastes schlegeli* embryo at stage 32, stained with ruthenium red. M = mitochondria, R = reticular network, O = apical opening and OC = outer cell.

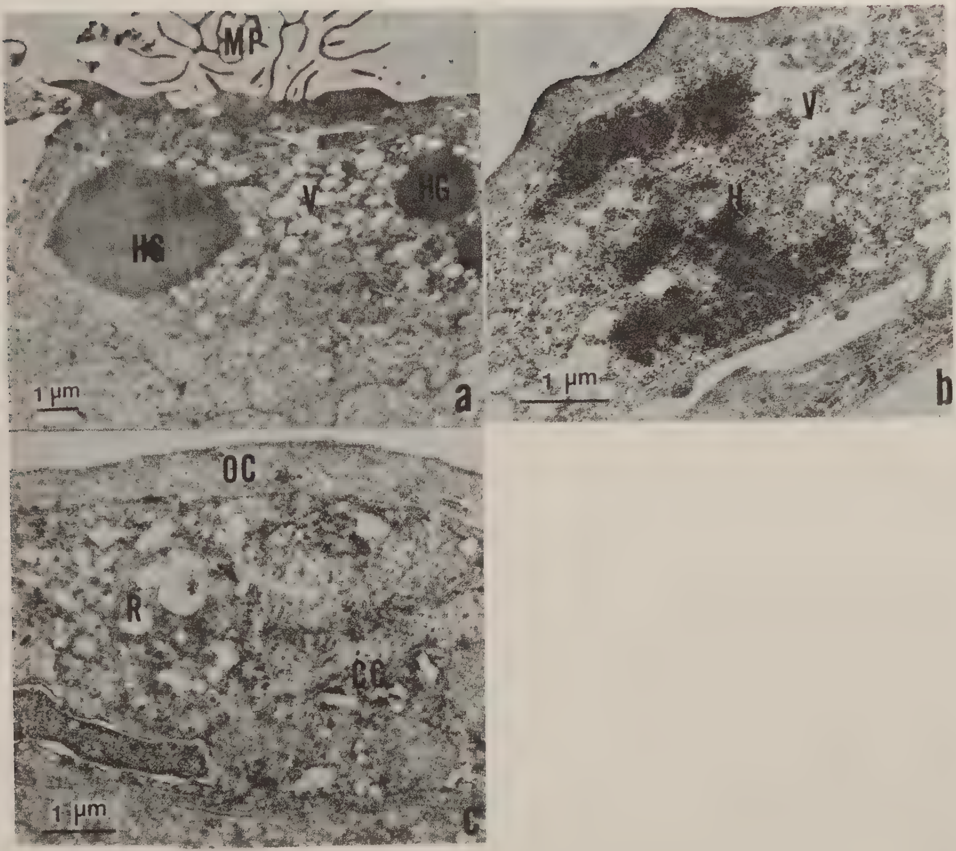

Fig. 5. Transmission electron micrographs of a *Sebastes melanops* embryo, treated with horseradish peroxidase (HRP): a – An outer epidermal cell with branched microvillous projections (MP) (stage 24). HG = large HRP globules, V = vesicles. b – An outer epidermal cell (stage 24). H = electron-dense HRP, V = vesicles. c – A chloride cell (CC) (stage 28) with electron-dense cytoplasm and expanded reticular network (R). OC = outer cell.

particles were present in the cytoplasm of the inner squamous cells (Fig. 1e). Numerous sacciform cells were anchored in the inner layer over the entire body surface and were particularly conspicuous in the dorsal and ventral finfolds.

In SEM profiles of the body surface of embryos around stage 28, sacciform cells were often characterized by a swollen appearance (Fig. 2a), whereas others were evident as depressions (Fig. 2b). The swollen sacciform cells contained fine, granular, moderately electron-dense materials in a large vacuole, which occupied the majority of the cytoplasm (Fig. 3). No deposition of RR was observed in these cells. Chloride cells rarely were observed in the inner layer of embryonic epidermis, but were conspicuous in larvae. No RR deposition was evident in the chloride cells, although their apical openings were dotted with RR particles (Fig. 4).

In embryos of *S. melanops* treated with HRP in toto, the main body surface was stained strongly with brownish HRP. The finfold was pale brown. Transmission electron microscopy revealed that some outer epidermal cells contained inclusions of electron-dense HRP (Fig. 5a). Branched microvillous projections were visible at the apical surface of these cells. Other cells contained electron-dense

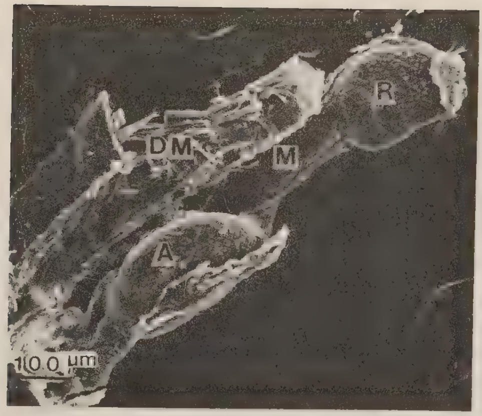

Fig. 6. Scanning electron micrograph of the embryonic digestive tract of *Sebastes schlegeli* at stage 28. A = anterior gut, DM = dorsal muscle, M = midgut and R = rectum.

HRP that appeared to be diffusing in the cytoplasm (Fig. 5b). However, most of the outer epidermal cells revealed no intracellular HRP. Chloride cells revealed no signs of HRP (Fig. 5c).

Digestive tract

In embryos of *S. schlegeli* during the late stages, epithelial cells of the rectum contained an amorphous granular substance, which has been described by Shimizu & Yamada (1980) and suggested to be evidence of the absorption of exogenous nutrients (Boehlert et al. 1986). In embryos at stage 28, the digestive tract had a hindgut or rectum that was distinguishable from the midgut by its enlarged appearance (Fig. 6). The anterior midgut was differentiated into several parts with varying diameters and a few constrictions. The mouth and the anus were already open. The rectum was separated from the midgut by a valve composed of an epithelial fold. The rectal epithelium consisted of high pseudostratified columnar cells, which had numerous microvilli forming a well-developed, striated border at the apical surface (Fig. 7a). Numerous pinocytotic invaginations were seen between the bases of adjacent microvilli. Amorphous or fine, granular electron-dense materials were present in the invaginations as well as in the rectal lumen. Some invaginations formed coated vesicles. In the apical cortex, many tubular structures containing electron-dense materials collectively constituted a canalicular system. Numerous vesicles of various sizes were confined to the subapical region. Large globules, apparently formed by fusion of the vesicles, were distributed in the supranuclear zone. Some globular inclusions were filled with electron-dense materials, while others were empty or partially filled. Inclusions that appeared to be degrading were present near the nucleus. Similar inclusions were found also in a large Golgi field (Fig. 7b).

When treated with HRP, the digestive tract, especially the rectum, was stained dark brown, indicating active uptake of HRP (Fig. 8a). Vesicles containing HRP were observed by TEM in the rectal cells (Fig. 8b). Small degrading HRP inclusions were observed near the lateral and basal membranes, but no Golgi apparatus was associated with these inclusions. Fine, electron-dense granules were conspicuous in the cytoplasm.

Discussion

As in our study, numerous inclusions of electron-dense substances and their degradation products have been observed in the rectal cells of *S. schlegeli* embryos at stage 28 (Boehlert et al. 1986). *Sebastes melanops* embryos treated with HRP have a conspicuous accumulation of tracer in the digestive tract, especially in the rectum. The embryos at stage 28 are characterized by the opening of the mouth and the anus (Yamada & Kusakari 1991). Therefore, the observations indicate that orally ingested materials are actively absorbed by the rectal cells in the same pinocytotic process described in HRP-injected larvae of *Cottus nozawae* by Watanabe (1984). The ingesta in viviparous *Sebastes* embryos with a functional mouth probably are derived from the ovarian fluid. Substances absorbable in the rectal cells are probably high molecular weight protein complexes, such as glycoproteins and lipoproteins, because contents of the inclusions varied in texture.

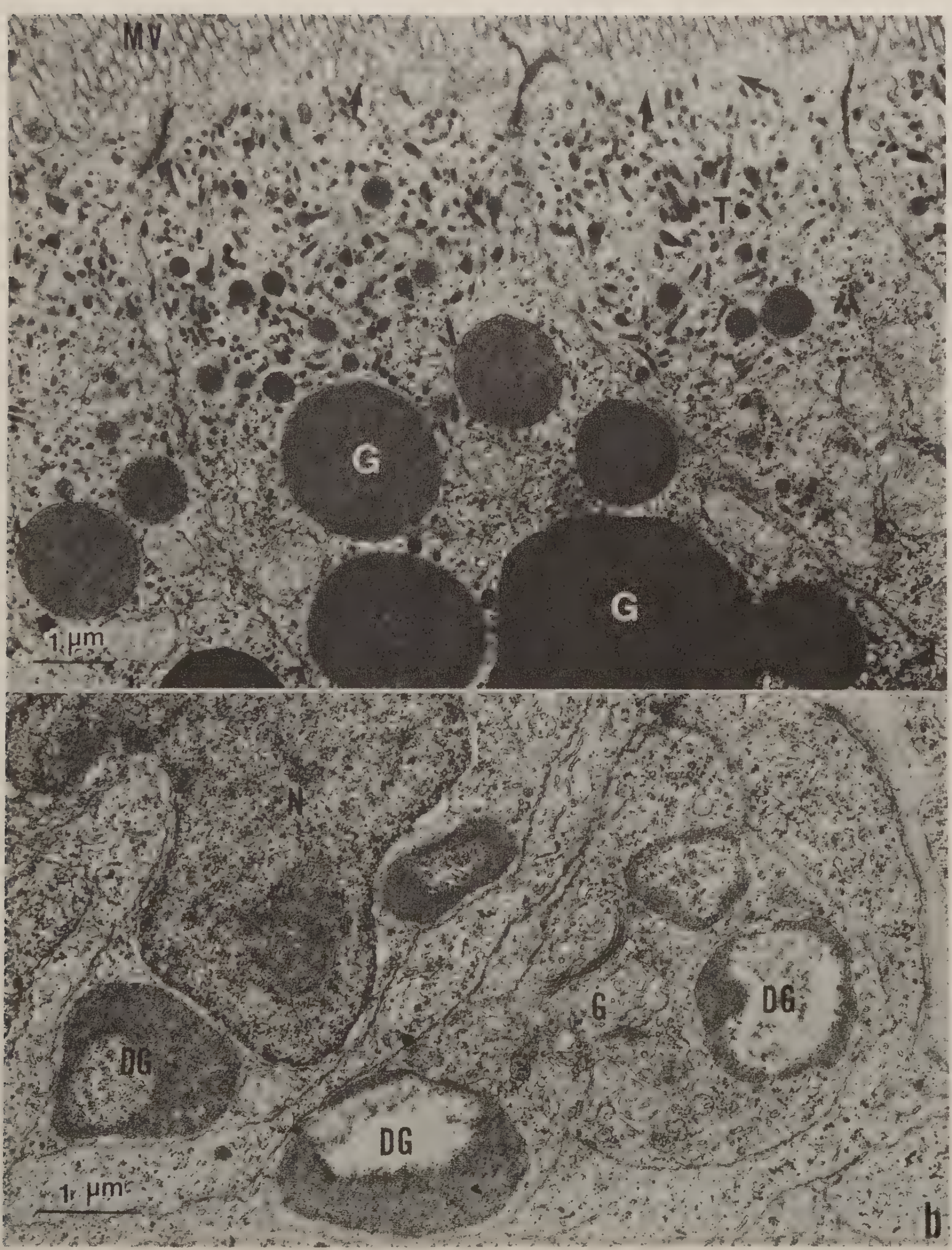

Fig. 7. Transmission electron micrographs of a *Sebastes schlegeli* embryo at stage 28, stained with ruthenium red: a – Embryonic rectal cells actively taking up external materials. G = electron-dense globules in the supranuclear region, MV = microvillus, T = tubular structures, Arrow = pinocytotic invagination. b – A rectal cell with degrading globules (DG) in a large Golgi field (G). N = nucleus.

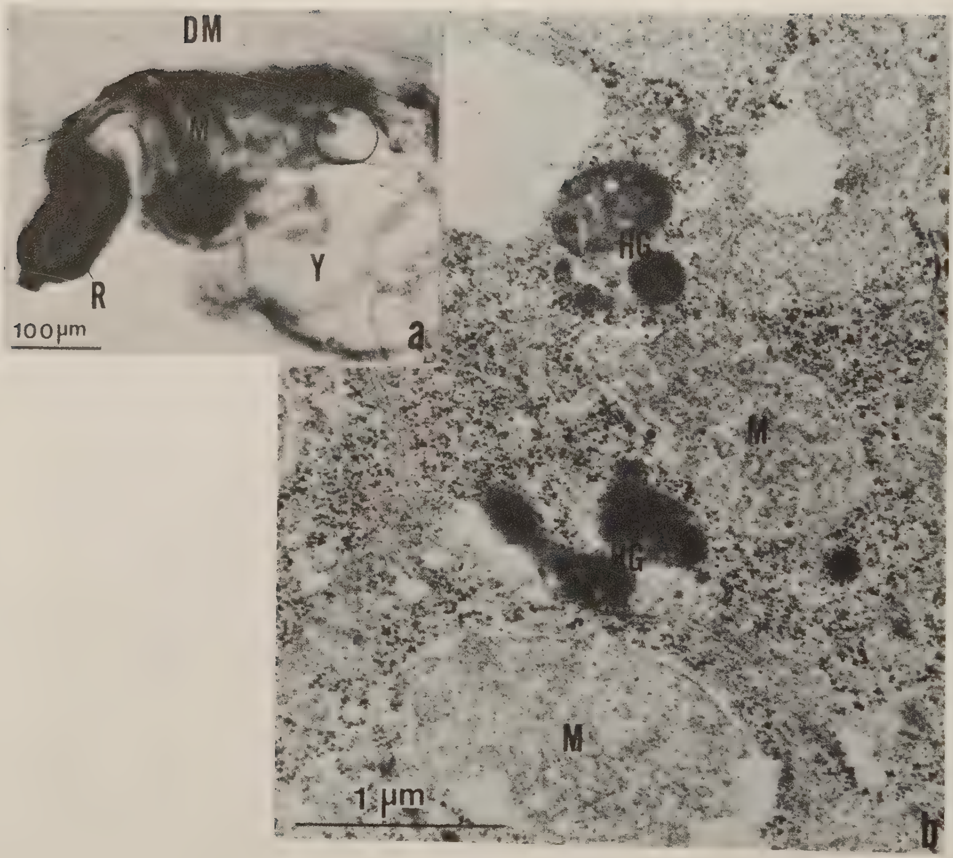

Fig. 8. Sebastes melanops embryos at stage 28, treated with horseradish peroxidase (HRP): a – Light micrograph of the embryonic digestive tract with abundant HRP, DM = dorsal muscle, M = midgut, R = rectum and Y = yolk sac. b – Transmission electron micrograph of a rectal cell containing globules of HRP (HG) among mitochondria (M).

The epidermis of *Sebastes* embryos at the late stages consists of two cell layers, as do the embryos of *Oncorhynchus keta* (Aso et al. 1977) and larvae of *Clupea harengus* (Jones et al. 1966) and *Hypomesus olidus* (Yamada 1968). The outer epidermal cells allow infiltration of RR, a tracer known to be impermeable to cell membranes and commonly used as a marker substance to show intercellular spaces (Brooks 1969). This suggests that at least the outer cell layer of the embryonic epidermis of *Sebastes* is permeable to some low weight molecules contained in the intraovarian environment. In addition, the outer cells commonly have well-developed tubular structures, which probably consist of cisternae of the ER. Similar structures have been described as the tubular-cisternae complex in the trophotaenial epithelium of the viviparous teleost *Characodon eiseni* (Mendoza 1972). Membranes of the tubular system of *Sebastes* embryos in our study were dotted with RR, suggesting that this membrane system opens outward at the apical surface.

Incubation of live embryos (stage 24) with HRP proved that some epidermal cells can take up exogenous, high weight molecules. These cells, characterized by well-developed microvilli, were not commonly found in all examined embryos. In embryos of stages 21, 28 and 31, such microvilli-bearing epidermal cells have not been reported (Boehlert & Yoklavich 1984, Boehlert et al. 1986). Stages 24 and 25 are the midpoint in epidermal cell differentiation from a smooth surface (stage 21) to developing numerous microridges (stage 28), which are probably involved in the initial uptake of external nutrients. The lack of involvement of sacciform cells in material uptake suggests that the cells are not absorptive, and we cannot speculate on their function.

The morphological features observed in the present study indicate that the embryonic epidermis is structurally loose and absorbs low molecular weight substances, whereas the rectal cells are involved in active uptake of high molecular weight substances after the opening of the mouth. Further research with specified substrates will be necessary to define the source and identity of such substances.

Acknowledgements

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References cited

Aso, N., H. Saito & T. Takagi. 1977. Microridge formation of epidermal cells of the developing salmon (*Oncorhynchus keta* Walbaum): scanning and transmission electron microscopic study. Zool. Mag. 86: 208–221. (In Japanese.)

Boehlert, G.W., M. Kusakari, M. Shimizu & J. Yamada. 1986. Energetics during embryonic development in kurosoi, *Sebastes schlegeli* Hilgendorf. J. Exp. Mar. Biol. Ecol. 101: 239–256.

Boehlert, G.W. & M.M. Yoklavich. 1984. Reproduction, embryonic energetics, and the maternal-fetal relationship in the viviparous genus *Sebastes* (Pisces: Scorpaenidae). Biol. Bull. 167: 354–370.

Brooks, R.E. 1969. Ruthenium red stainable surface layer of lung alveolar cells: electron microscopic interpretation. Stain Tech. 44: 173–177.

Iwai, T. 1969. Fine structure of gut epithelial cells of larvae and juvenile carp during absorption of fat and protein. Arch. Histol. Jap. 30: 183–199.

Jones, M.P., F.G.T. Holliday & A.G.E. Dunn. 1966. The ultrastructure of the epidermis of larvae of the herring (*Clupea harengus*) in relation to the rearing salinity. J. Mar. Biol. Ass. U.K. 46: 235–239.

Karnovsky, M.J. 1965. A formaldehyde-glutaraldehyde fixative of high osmolarity for use in electron microscopy. J. Cell Biol. 27: 137A.

Mendoza, G. 1958. The fin fold of *Goodea luitpoldii*, a viviparous cyprinodont teleost. J. Morph. 103: 539–560.

Mendoza, G. 1972. The fine structure of an absorptive epithelium in a viviparous teleost. J. Morph. 136: 109–130.

Shimizu, M. & J. Yamada. 1980. Ultrastructural aspects of yolk absorption in the vitelline syncytium of the embryonic rockfish, *Sebastes schlegeli*. Jap. J. Ichthyol. 27: 56–63.

Tanaka, M. 1969. Studies on the structure and function of the digestive system in teleost larvae-2. Characteristics of the digestive system in larvae at the stage of first feeding. Jap. J. Ichthyol. 16: 41–49. (In Japanese.)

Turner, C.L. 1947. Viviparity in teleost fishes. Sci. Mon. 65: 508–518.

Veith, W.J. 1979. The chemical composition of the follicular fluid of the viviparous teleost *Clinus superciliosus*.Comp. Biochem. Physiol. 63A: 37–40.

Veith, W.J. 1980. Viviparity and embryonic adaptations in the teleost *Clinus superciliosus*. Can. J. Zool. 58: 1–12.

Watanabe, Y. 1982. Intracellular digestion of horseradish peroxidase by the intestinal cells of teleost larvae and juveniles. Bull. Jap. Soc. Sci. Fish. 48: 37–42.

Watanabe, Y. 1984. An ultrastructural study of intracellular digestion of horseradish peroxidase by the rectal epithelium cells in larvae of a freshwater cottid fish *Cottus nozawae*. Bull. Jap. Soc. Sci. Fish. 50: 409–416.

Wourms, J.P., G.D. Bryon & J. Lombardi. 1988. The maternal-embryonic relationship in viviparous fishes. pp. 1–134. *In:* W.S. Hoar & D.J. Randall (ed.) Fish Physiology, Vol. 11B, Academic Press, New York.

Yamada, J. 1968. A study on the structure of surface cell layers in the epidermis of some teleosts. Annot. Zool. Jap. 41: 1–8.

Yamada, J. & M. Kusakari. 1991. Staging and the time course of embryonic development in kurosoi, *Sebastes schlegeli*. Env. Biol. Fish. 30: 103–110.

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Estimates of Age and Growth of Ehu *Etelis carbunculus* in Four Regions of the Pacific from Density of Daily Increments in Otoliths

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Abstract.–Growth of the deep slope snapper *Etelis carbunculus* was evaluated from the density of daily increments in sagittal otoliths collected from Hawaii, the Commonwealth of the Northern Marianas Islands (NMI), French Polynesia, and Vanuatu. The rate of otolith growth (μm/day) as a function of otolith radius was fit by regression to a modified Gompertz rate curve and the age of fish estimated by integrating the equation. There were slight regional differences between the estimated values of each of the three otolith growth rate parameters, which may be attributable in part to random sampling differences. However, integrated estimates of fish age versus otolith radius varied little between sites because of the compensatory relationship between two of the three estimated parameters which together determine the rate of dampening of the otolith growth function. There were significant regional differences in average otolith radius, and thus in estimated age, as a function of fish length. Fish from Vanuatu and NMI were younger at a given length than those from the other two regions. However, fish as large as those at Vanuatu are not found at NMI, suggesting there may be regional differences in mortality. Regional age-at-length data were fit to a von Bertalanffy growth curve, both unconstrained and held to a value of asymptotic length (L_∞) obtained from the literature. Estimates of natural mortality for each region are discussed, based on the regional values obtained for the von Bertalanffy growth constant (K). These results should be confirmed using data obtained from a wider range of fish sizes.

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The observation of microscopic markings in thin sections of the otoliths of fishes, with evidence that these marks present a record of daily growth (Panella 1971, 1974), provided an alternative means of ageing tropical species for which seasonal and annual growth rings are often hard to interpret. These marks are produced in many fishes (Brothers et al. 1976, Struhsaker and Uchiyama 1976, Wild and Foreman 1980, Neilson et al. 1985, Jones and Brothers 1987, and others). Counting otolith microincrements has proved useful in estimating the growth of juvenile and larval fishes (Barkman 1978, Methot 1981, McGurk 1984, Jones 1986, Geffen 1986), because they have small and transparent otoliths with readily interpretable microincrements. While offering the opportunity to detect growth on a more sensitive scale, the laborious process of enumerating all the daily increments in the otoliths of older organisms has limited the widespread use of this technique (Ralston and Williams 1988a).

From the late 1970s through the mid- and late 1980s, Ralston and colleagues (Ralston 1976, 1981, 1985; Ralston and Miyamoto 1981, 1983; Ralston and Williams 1988a) developed a labor-efficient method of estimating the age and growth rate of fishes using microincrement data from otoliths. This method, based on numerical integration of otolith growth rates from the density of presumptive daily increments, was applied by S. Ralston and H.A. Williams (Honolulu Lab., NMFS Southwest Fish. Sci. Cent., Honolulu, HI, unpubl. data) to a number of Pacific Ocean commercial species. It provided an estimate of the von Bertalanffy (1957) growth curve for which the asymptotic length (L_∞), growth constant (K), and age at zero length (t_0) were within the range of previous regional estimates for many of the 24 species for which the method was tested.

However, three out of four growth curves estimated by this method for the deep slope "red" snapper *Etelis carbunculus* (known as ehu in Hawaii), did not reach an asymptotic length, instead having the form of a straight line with positive slope. These results were considered to be anomalous, since collections included fish at or near the regionally estimated values of asymptotic length (although the sample size for some regions was very small). Otolith collections for this species came from Hawaii, Vanuatu, French Polynesia, and the

Commonwealth of the Northern Marianas Islands (NMI). In the single case where the estimated von Bertalanffy growth curve did reach an asymptote (379 mm for NMI), it did so considerably below the maximum length commonly found in that region (580 mm) and well below the maximum length included in the data.

The present study reevaluated the method of age and growth estimation using the same data, in an attempt to see if growth estimates could be improved. In response to some of the problems encountered in reprocessing the data, the methodology of integrating and fitting was modified in a manner that may prove useful to other researchers. In addition, some important guidelines for collecting data for growth estimation from integrated microincrement densities were developed.

Methods

Ralston and Williams' otolith growth data (unpubl.) from Hawaii, Vanuatu, French Polynesia, and NMI were reevaluated, using a new method that employs both analytical and numerical integration of the rate curve. Fork lengths were recorded and sagittal otoliths removed from fish caught with bottom handlines at depths of 80–200 m in the four regions. The data were collected and compiled by Ralston and Williams from 1982 to 1988. They collected a wide size range of fish, but made no systematic sample of a representative number of organisms of each size. Small fish, not ordinarily captured with the large hooks used by commercial fishers, were underrepresented in all regional samples. Collections were essentially random, within the size range selected by this fishing gear. Since the principal objective was to find an appropriate method of fitting and integration, this limitation was acceptable.

Otoliths were prepared and microincrement densities on the postrostral axis recorded from video-relayed images using techniques described by Ralston and Williams (1988a). The data available for each fish included fork length, total otolith postrostral radius, and a series of estimates of microincrement density at various points along the otolith radius. Microincrement densities were registered in microns per increment, calculated by dividing the length of the radial segment by the number of increments counted within it. Following the assumption of Ralston and Williams (1988a) and Brouard et al. (1983) that microincrements are deposited on a daily basis for *Etelis carbunculus*, increment densities represent otolith growth rate (microns/day) as a function of distance from the origin of growth, or focus. Validation of daily increment deposition for most deep slope snappers has not been obtained because of low survival when fish are brought to the surface. However, validation was obtained for *Pristipomoides filamentosus* (Ralston 1981), another eteline snapper found in similar habitat and locations.

Ralston's method of age integration consists of estimating the time transpired within consecutive 500-μm intervals of otolith radius, by multiplying the length of each interval by its mean growth rate (microns/day). The estimated number of days required to grow through each 500-μm radial interval are then summed numerically, producing a series of estimated ages for fish with otoliths measuring 500, 1000, 1500 μm, etc. The relationship between the natural logarithms of fork length and otolith radius, determined by regression from each regional sample, is then used to estimate fish length at the midpoint of each 500-μm interval of otolith radius. The resultant age-at-length data are fit to a von Bertalanffy growth curve by nonlinear regression. In this way, estimated fork lengths for a hypothetical group of fish with otoliths measuring 250–9250 μm (by intervals of 500) are fit to age estimates for otoliths at 500–9500 μm (by 500-μm intervals). Actual fork lengths and otolith measurements are used only to estimate the relationship between fork length and otolith radius. In addition to the slight difference in otolith radius (250 μm) between age and length estimates, the validity of the assumption that the length of fish as a function of otolith radius can be accurately predicted from a regression curve obtained from the original sample depends on having had a representative size range and number of individuals from each population. Rather than incorporate this sampling error, it was decided to concentrate on using the otolith growth-rate data to obtain integrated age estimates for the fish and otoliths sampled.

Early attempts at integrating the otolith growth function were aimed at reducing the size of the radial interval used to approximate the growth rate. This was found to be impractical for various reasons. The average number of microincrement density estimates ("readings") per fish ranged from 4.1 to 61.5 regionally. Otoliths from Hawaii and French Polynesia were measured more extensively; 1681 and 3877 readings were made from 37 and 63 otoliths, respectively. For NMI and Vanuatu, fewer measurements were made (252 and 141 from 62 and 13 otoliths, respectively). Because of these differences in the number and distribution of microincrement density readings along the otolith radius, the reliability of mean otolith growth rates and resultant age estimates varied widely as a function of the length of the radial interval chosen. The asymmetry of the otolith growth-rate function compounded this problem. Therefore, an alternative method of integration that did not rely on mean microincrement densities as a function of radial intervals was chosen.

Estimates of otolith growth rate as a function of radius were fit by SAS (1985) nonlinear regression to a modified Gompertz rate curve (Gompertz 1825, Winsor 1932) of the form

$$y = axe^{-bx} + c \qquad (1)$$

where y = estimated density of daily increments or otolith growth rate (μm/day),
x = radial distance (μm) at which each density was recorded,
a and b = shape parameters,
c = a constant representing the asymptotic otolith growth rate.

The Gompertz rate curve was chosen for its general shape and was then modified in form to provide a better fit to observed data. The constant was added because recorded microincrement densities did not subside to zero, instead reaching a low positive value.

Substituting dx/dt for y in equation (1) gives a clear picture of the otolith growth-rate function. Since the growth rate was estimated in days, the integral of the reciprocal of the righthand side of this function provides an estimate of the fish age in days as a function of otolith radius in microns, as follows:

Since $\quad dx/dt = axe^{-bx} + c$

then

$$t_x = \int_m^n \frac{dx}{axe^{-bx} + c} \qquad (2)$$

where m and n are any two distances along the otolith radius. Substituting $u = bx$ and $du = bdx$ gives

$$t_x = \int_{mb}^{nb} \frac{du/b}{(au/b)e^{-u} + c} \qquad (3)$$

$$= \frac{1}{cb} \int_{mb}^{nb} \frac{du}{(a/bc)ue^{-u} + 1}$$

$$= \frac{1}{cb} \int_{mb}^{nb} \{\sum_{k=0}^{\infty} ((a/bc)ue^{-u})^k (-1)^k\}\, du$$

$$= \frac{1}{cb} \sum_{k=0}^{\infty} (-1)^k \int_{mb}^{nb} [(a^k/b^kc^k)\, u^k e^{-ku}]\, du$$

$$= \frac{n-m}{c} + \sum_{k=1}^{\infty} \frac{(-1)^k a^k}{b^k c^k k^{k+1}} \Gamma(k+1, kmb)$$

$$- \sum_{k=1}^{\infty} \frac{(-1)^k a^k}{b^k c^k k^{k+1}} \Gamma(k+1, knb) \qquad (4)$$

where Γ is the incomplete gamma function and k is a dummy variable. The first term, representing the asymptotic growth rate, is solved separately. Using the ratio test for convergence and an estimate based on the Gaussian continued fraction

$$V^k e^{-V} < \Gamma(k+1, V) < \frac{(V^{k+1}e^{-V})}{V-k} \qquad (5)$$

(in Wall 1948), the first series converges for $mb>M$ and the second for $nb>M$, where M is a solution of

$$\frac{M^2e^{-M}}{M-1} = bc/va \quad \text{and } v \text{ is any number} >1. \qquad (6)$$

Thus, for each set of values of a, b, and c, a distinct point can be identified at which the expanded series converges quickly. For speed of computation, we chose $v = 2$, to ensure that the ratio of consecutive integrals would be less than 1/2. Age in days was estimated for each otolith radius by a Fortran program, adapted from Davis and Rabinowitz's (1984) routine for Romberg integration. Given values of x (otolith radius in microns), a, b, and c, the program first solves equation (6) by Newton's method (in Atkinson 1989) and then either uses the expanded series from equation (4), if it converges quickly, or evaluates the integral given in equation (3) by Romberg integration. Both estimates were made with a tolerance of 10^{-15}.

Fork lengths and estimated ages of the fish sampled were fit to the von Bertalanffy (1957) growth curve

$$L_t = L_\infty (1 - e^{-K(t-t_0)}),$$

where L_∞ and t_0 represent theoretical values of asymptotic length at infinite age and age at zero length, respectively; K is a growth constant; and t is fish age in years. The Marquardt method of iterative least-squares fitting was used, under SAS (1985) nonlinear fitting procedure. For comparison, the data were also fit by von Bertalanffy's method of log-linear regression, using a BASIC program by Gaschütz et al. (1988).

Table 1

Summary of otolith collections and maximum size of red snapper *Etelis carbunculus* by region.

Collection site	No. of otolith	Fork lengths (mm) Sampled Min.	Max.	Avg.	SD	Recorded or estimated MLR*	ML_∞**
Hawaii	37	226	641	428.2	101.6	700 (1)	718 (5)
Fr. Polynesia	63	160	510	351.5	82.0	680 (2)	—
No. Marianas	62	29	527	337.5	66.3	540 (3)	537 (6)
Vanuatu	13	270	920	520.8	194.4	1270 (4)	993 (7)

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*MLR = Maximum length recorded (from regional fishery statistics).

**ML_∞ = Average of three estimates of asymptotic length (L_∞) for the von Bertalanffy growth curve (from the literature).

Sources of MLR estimates

(1) United Fishing Agency, Ltd. (UFA), Honolulu, pers. commun., July 1988.
(2) Wrobel 1985
(3) National Marine Fisheries Service (NMFS), 1982–84. RAIOMMA Cruise data, unpubl. logs, NMFS Honolulu Lab.
(4) R. Grandperrin, ORSTOM fisheries biologist, Mission ORSTOM, New Caledonia, pers. commun., Feb. 1989.

Sources of ML_∞ estimates

(5) Ralston and Kawamoto 1987, Uchida et al. 1982
(6) Ralston and Williams 1988b, NMFS RAIOMMA data 1982–84
(7) Brouard et al. 1983, Brouard and Grandperrin 1985, Carlot and Nguyen 1989

Table 2

Estimated otolith growth-rate parameters and summary statistics for the modified Gompertz rate curve by region for red snapper *Etelis carbunculus*.

Location		Parameter estimate	±95% CI	Asymptotic correlation matrix a	b	c
Hawaii	a	0.0688	±0.00311	1	0.741	−0.038
	b	0.0018	0.00005	0.741	1	0.499
	c	2.4242	0.22536	−0.038	0.499	1
			*R^2 0.713, n 1680,	**RSS 14211		
French Polynesia	a	0.0991	0.00357	1	0.764	0.006
	b	0.0021	0.00004	0.764	1	0.474
	c	2.4086	0.17919	0.006	0.474	1
			R^2 0.647, n 3877,	RSS 58776		
Commonwealth Northern Marianas	a	0.1111	0.01365	1	0.881	0.335
	b	0.0021	0.00014	0.881	1	0.624
	c	2.2672	0.43602	0.335	0.624	1
			R^2 0.824, n 252,	RSS 1251		
Vanuatu	a	0.0702	0.01180	1	0.866	0.204
	b	0.0019	0.00017	0.866	1	0.502
	c	2.1076	0.41886	0.204	0.502	1
			R^2 0.801, n 141,	RSS 467		
Overall (all locations combined)	a	0.0884	0.00250	1	0.765	0.012
	b	0.0020	0.00003	0.765	1	0.489
	c	2.3961	±0.13758	0.012	0.489	1
			R^2 0.661, n 5941,	RSS 76799		

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*Multiple correlation coefficient $R^2 = [\Sigma(\hat{Y}_i - \bar{Y})^2/\Sigma(Y_i - \bar{Y})^2]$

**RSS = Residual sum of squares

Results

Number of otoliths, fish size range, and locations of collections are summarized in Table 1. For comparison, the maximum length registered in fisheries landings (MLR) and mean of available estimates of asymptotic length (ML_∞) for each region and their sources are also included. Intermediate sizes were represented in the data from most regions, but extremely large or small fish were underrepresented or lacking. The sample from Vanuatu was very small, but encompassed a wider range of fish lengths than was sampled from any other location. The limitations of the data must be kept in mind in interpreting and comparing results.

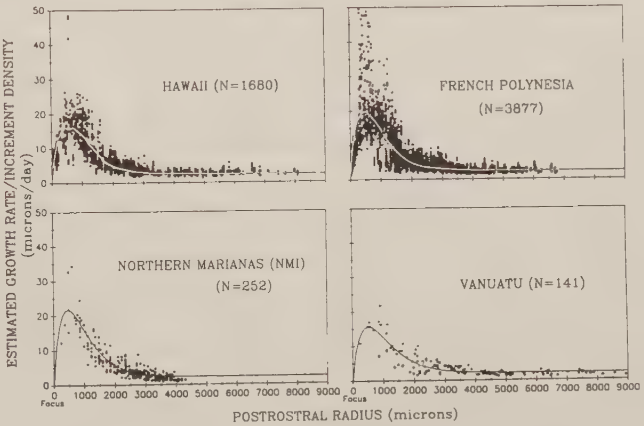

Figure 1

Estimated otolith growth rate and recorded microincrement densities for red snapper *Etelis carbunculus*.

Nonlinear regressions of otolith growth rate versus otolith radius in microns (Table 2) produced estimates of the parameters a, b, and c of the rate equation, with asymptotic 95% confidence intervals. Multiple correlation coefficients were calculated for each regression as an additional index of fit. Data were pooled for all locations to estimate a global rate for otolith growth. The multiple correlation coefficients are low for these curves, due to the wide range of variation in recorded increment density near the focus (high residual variance). Predicted curves and recorded microincrement densities for each region were compared (Fig. 1). The function chosen mimics the behavior of the rate curve fairly well; however, the fit could be improved in the descending portion of the curve between 500 and 1500 μm of otolith radius. Few readings were made close to the otolith focus ($<246\,\mu$m) for NMI and Vanuatu samples (Fig. 1). Fitting the data to the rate curve assumes that these otoliths grew similarly to those for which the ascending portion of the curve was sampled. The fit for the descending portion of the curve is supportive of this assumption. However, since the widest range of variation in recorded microincrement densities was always found close to the focus, these results should be interpreted cautiously.

Predicted ages at equal otolith radius, using the parameters in Table 2, were calculated for each region (Table 3a). Although there were differences between the estimated regional otolith growth parameters, predicted ages as a function of otolith radius were generally similar. The relationship between the shape parameters a and b is such that differences between them can be compensatory, one (a) controlling the amplitude of the rate curve and the other (b) the rate of dampening. The radius at which peak otolith growth rate is estimated (the maximum of the otolith growth-rate function) was similar regardless of region or weighting. Peak growth rate occurs where the derivative of $axe^{-bx} + c$ is equal to zero, or at $x = 1/b$. Estimated ages for this radial distance are included in Table 3a, where it can be seen that the otoliths of ehu from all regions reach their maximal growth rate between 1 and 2 months of age. Otoliths reach a constant growth rate before fish are 1.5 years old, or between 3000 and 3500 μm of otolith radius.

For comparison, the age estimates made by Ralston and Williams for comparable 500-μm intervals of otolith radius are given in Table 3b. The values are similar in many respects for Hawaii and French Polynesia (where more microincrement density estimates were made), but there are observable differences for all regions. Ralston and Williams' age estimates were lower close to the otolith focus, the two estimates were equivalent at intermediate radius, and their estimates were again lower at greater otolith radius. The exception to this pattern was seen for Vanuatu, for which our estimates were substantially lower at maximum radius. The radius at which the two estimates were equivalent and the magnitude of the difference between them varies from one region to another and is a function of the amount and variability of microincrement density readings and their effects on both estimates. The best check of which method gave more accurate results would be

Table 3A

Predicted ages at equal radial distances from estimated otolith growth rates for the red snapper *Etelis carbunculus*. NMI = Northern Marianas.

Otolith radius (μm)	Estimated age (days)				
	Hawaii	F. Poly.	NMI	Vanuatu	Overall
10	3.2	3.1	3.2	3.5	3.1
100	20.0	16.9	16.4	21.0	17.9
500	50.2	40.7	38.5	51.8	43.6
1000	82.4	68.6	65.3	85.7	72.8
1200	98	83	80	102	88
1400	116	101	98	122	106
1600	137	123	120	146	128
1800	163	150	147	174	154
2000	193	182	181	208	186
2500	290	292	298	319	292
3000	423	441	457	472	437
3500	586	619	648	657	611
4000	769	813	855	865	804
4500	964	1015	1071	1084	1005
5000	1164	1220	1289	1309	1211
6000	1573	1634	1729	1766	1627
7000	1985	2049	2170	2225	2044
8000	2398	2464	2611	2684	2461
9000	2810	2879	3052	3144	2878
10000	3223	3294	3493	3603	3296
11000	3635	3710	3934	4063	3713
12000	4048	4125	4375	4523	4130
13000	4460	4540	4816	4982	4548
14000	4873	4955	5257	5442	4965
	Age at 1/b μm of otolith radius				
Age (days)	555.5	484.8	467.7	532.5	504.8
1/b	53.5	39.9	37.0	53.9	43.8

Table 3B

Ralston and Williams' age estimates at equal otolith radius for the red snapper *Etelis carbunculus*.

Otolith radius (μm)	Estimated age (days)			
	Hawaii	F. Poly.	NMI	Vanuatu
500	46.7	40.7	25.1	37.5
1000	76.7	68.2	51.6	69.3
2000	193	191	172	211
2500	289	295	272	311
3000	422	416	418	433
3500	570	568	622	580
4000	758	764	866	759
4500	937	960	1250	1006
5000	1119	1157		1276
6000	1479	1571		1937
7000	1795	1955		2663
8000	2158			3181
9000				3997

to count all microincrements to a specific radius for the same otoliths. This was beyond the scope of the present study.

Fork lengths and age estimates, obtained by integrating the rate curve over the corresponding otolith radius (Appendix 1), were fit to a von Bertalanffy growth curve (Table 4). Both unconstrained regression and regressions with constraints on asymptotic length (L_∞) or age at zero length ($t_0 = 0$) were tested. Regressions with the highest indices of correlation were generally obtained by forcing the curve through an estimate of asymptotic length obtained from the literature or from regional fisheries statistics. The greatest value of MLR or ML_∞ from Table 1 for each region was used as an approximation of an appropriate forcing value. The criterion for convergence was based on a minimum level of improvement in the ratio of subsequent sum of squares errors (SSE):

$$(SSE_i - SSE_{i-1})/(SSE_i + 10^{-6}) < 10^{-8}.$$

Regressions which didn't converge after 200 iterations were eliminated. NMI was the only region for which the regression was able to converge with the constraint that $t_0 = 0$. Two fish from French Polynesia were omitted from the data, because their otolith radial lengths were not recorded.

Log-linear regressions using the Gaschütz et al. (1988) BASIC program were also done for comparison. These are weighted regressions of average age-at-length for NMI and French Polynesia, which had more than 50 observations. Figure 2 shows the best four growth curves (from Table 4). For all regions except NMI, these were the nonlinear regressions constrained in L_∞. The nonlinear method of fitting was preferred because it involved no artificial reduction of the variance observed in the data. For NMI the nonlinear regression constrained only to $t_0 = 0$ was used, because it had a higher r^2 value and lower residual variance. None of the curves for NMI showed a good fit; these results are included for comparison.

The scatterplot of age-at-length data (Fig. 2) illustrates the limitation on regression estimates imposed by the size range and number of fish sampled for each region. The most significant constraints on fitting a growth curve to the data were the high variance of estimated age (otolith radius) as a function of fork length, particularly for NMI and French Polynesia, and the limited range of fish sizes sampled. It was necessary to constrain most of the growth curves to an independently estimated value of L_∞, since there were few data points to represent extremely large or small fish. Although unconstrained curves could be fit to the data for Hawaii and French Polynesia, these reached values of L_∞ far above lengths of fish captured in these regions throughout the history of their fisheries. For NMI and Vanuatu, nonlinear regressions tended towards unlimited L_∞. These results were similar to those of Ralston and Williams, indicating that the primary limitation on accurate growth estimation was probably the range of fish lengths sampled.

However, the present regressions differ from those of Ralston and Williams' in that they are derived from age estimates for measured otoliths and fork lengths, rather than from estimated lengths at equally spaced intervals along the otolith radius. Ralston's method produces an artificially broader and more uniform sample. This is evident in that the one region (NMI) for which the previous estimate was able to converge showed an inadequate fit by the present method, which is consistent with the clustering of data points in the middle of the size range (Fig. 2). Experimental fitting to a Gompertz curve was done initially, but it was found that lack of fit by either method was more attributable to the variance in age estimates and the narrow range of fish sizes than to the choice of a growth curve. The regression of otolith radius on fork length was allometric for all regions examined, so it is not surprising that somatic growth rate is represented as well by the von Bertalanffy curve.

The von Bertalanffy growth constant (K) for the best curves for each region were in the range of 0.129–0.137 for Vanuatu, 0.179–0.310 for NMI, 0.064–0.190 for Hawaii, and 0.039–0.145 for French Polynesia. The highest value of K = 0.464 for NMI, estimated by log-linear regression, was arbitrarily left out of the range for this region as being abnormally high. Any of the estimates for NMI could well be excluded on the basis of the r^2 values. Estimates of natural mortality (M) for these K values using the relationship for snappers and groupers by Ralston (1987) and for various taxa by Ricker (1973) are listed in Table 5. These K estimates agree with those summarized by Manooch (1987) for other species of lutjanids, including several of the subfamily etelinae.

Table 4

Summary of estimated growth by region for the red snapper *Etelis carbunculus*.

Region/Fitting assumptions	L_∞ (mm)	t_0 (yr)	K	R^2	RSS*
Hawaii (*N* 37)					
von Bertalanffy (unconstrained)	1182.8	2.06	0.064	0.920	30507
von Bertalanffy fix L_∞ = 718 mm	718.0	3.32	0.163	0.874	35005
von Bertalanffy fix L_∞ = 718 (linear**)	718.0	4.03	0.190	0.884	44250
Vanuatu (*N* 13)					
von Bertalanffy (unconstrained)	(no convergence)				
von Bertalanffy fix L_∞ = 1270 mm	1270.0	1.41	0.129	0.911	37503
von Bertalanffy fix L_∞ = 1270 (linear)	1270.0	1.62	0.137	0.920	39095
French Polynesia (*N* 60)					
von Bertalanffy (unconstrained)	1458.6	1.13	0.039	0.784	86365
von Bertalanffy fix L_∞ = 680 mm	680.0	2.35	0.126	0.756	89370
von Bertalanffy fix L_∞ = 680 (linear)	680.0	3.05	0.145	0.837	65115
Northern Marianas (*N* 62)					
von Bertalanffy (unconstrained)	(no convergence)				
von Bertalanffy (linear/unconstrained)	750.0	−0.18	0.179	0.576	115656
von Bertalanffy fix L_∞ = 540 mm	540.0	−0.23	0.289	0.435	142350
von Bertalanffy fix L_∞ = 540 (linear)	540.0	0.94	0.464	0.519	130986
von Bertalanffy fix L_∞ = 540, t_0 = 0	540.0	0.00	0.310	0.504	143137
von Bertalanffy fix t_0 = 0 (only)	583.2	0.00	0.273	0.572	142493

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* RSS = Residual sum of squares.

** Linear = Log-linear regression and linear correlation coefficients from Gaschütz et al. (1988) BASIC program.

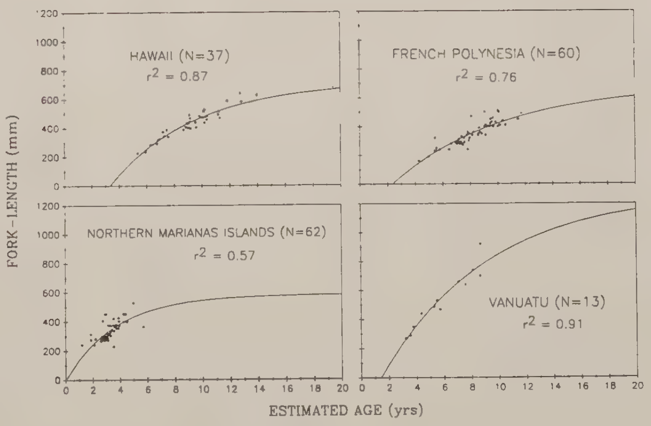

Figure 2

Estimated regional von Bertalanffy growth curves for red snapper *Etelis carbunculus*.

Table 5

Best estimated von Bertalanffy growth constant (K) and corresponding natural mortality estimates by region for the red snapper *Etelis carbunculus*.

	Range of best K estimates	Estimated natural mortality (M)	
		Ralston (1987)*	Ricker (1973)*
Hawaii	0.064–0.190	0.301–0.410	0.279–0.412
Vanuatu	0.129–0.137	0.285–0.301	0.258–0.279
French Polynesia	0.039–0.145	0.099–0.318	0.032–0.299
Northern Marianas	0.179–0.310	0.388–0.658	0.384–0.715

* Sources of regressions used to estimate natural mortality rate (M) from the value of the von Bertalanffy growth constant (K).

Discussion

The method presented is a variation on previous techniques of obtaining age estimates from microincrement densities (Methot 1983, Ralston and Williams 1988a, Gauldie et al. 1989). It provides a direct estimate of the fit of the rate function used to approximate the otolith growth curve, which is then integrated essentially without error. Part of the difficulty in comparing the present age estimates with those of Ralston and Williams was that a direct measure of error was not available for their estimates. Within the constraints of the fit of each rate curve, the present technique provides an accurate estimate of age at any chosen interval of otolith radius. The method also allows age estimation from the otolith focus to its perimeter, where readings become difficult, and gives a reliable estimate of the time transpired between any two points on the otolith radius.

The error introduced in numerical integration by the trapezoid method, dividing the otolith radius into increments of equal length and using the mean growth rate in each interval to estimate age, is well understood (Salas et al. 1986, Atkinson 1989). Most alternative methods of numerical integration have been developed to reduce the error introduced by the trapezoid estimate. Romberg's method is one of the most effective ways of eliminating this error, evaluating and subtracting it out as part of the process of integration. The result is a negligible integration error for the purposes of this discussion. The error in the present method derives from natural variability in otolith growth rates, lack of fit of the chosen rate curve, and any inadequacies in the data. The first two sources of error are measured by the sums of squares, and are represented in the multiple correlation coefficient and asymptotic confidence intervals for parameter estimates. Thus, another advantage of the present method is that alternative curves can be fit to evaluate the advisability of using other functions or combinations of functions to fit the data.

The reliability of these growth estimates is dependent, among other things, upon the assumption that Ralston and Williams were able to count all or most of the increments present in the otoliths at a given radius. This is true to a varying extent; however, the reliability of the readings may decrease as fish get older. Most microincrement density measurements were made within 50–60% of the total otolith radius. However, in each region, there were "legible" segments near the perimeter of some otoliths. The sectioning techniques and optical resolution of the Nikon light microscope and RCA video system used to observe the slides were sufficient to see detail considerably below the scale on which microincrements were recorded. Therefore, we believe that any error in the data is unlikely to have been derived from a failure to observe increments that were present.

Some error in measuring total otolith radius may have occurred, however, due to changes in the orientation of growth along the postrostral axis as fish get larger. Difficulties in reading otolith microincrements in older fish, induced by the transformation in shape and crystalline structure of the otolith affect the legibility of daily increments (Radtke 1987, Davies et al. 1988). Thus an important follow-up to these preliminary estimates is to confirm the orientation of the postrostral growth axis as a function of otolith size for each region. The hypothesis that otolith growth rate is essentially constant beyond a certain radius could be tested by reexamining microincrement densities for some of the larger otoliths near their perimeter.

A difference in actual microincrement densities at maximum otolith radius would influence age estimates significantly. An unmodified Gompertz rate curve (without the constant) was used in early attempts at fitting microincrement densities. This curve fit the data fairly well for small otolith radius, but the decline of the rate curve to zero at greater radius provided a poor fit and caused age estimates for large fish to increase by more than an order of magnitude. A constant was added to the rate curve for these reasons, significantly improving the fit and bringing age estimates into conformity with other estimates by fishery biologists and experienced fishers.

The growth estimates presented can be improved by sampling a wider size range and larger number of organisms and by recording microincrement densities along the full length of the radial axis of all otoliths sampled. For very small fish, increments near the focus can be counted and integration is not necessary to get an age estimate. The size of the sample would be determined by the variance of otolith radius as a function of fork length, a characteristic which varies regionally. Otolith radius, and thus estimated age, was highly variable for a given fork length for all regions for which a sufficiently large sample was available to make this determination. This is evidence that a fairly large sample is necessary in order to have a reliable growth estimate. Sampling a representative number of fish within a full range of sizes and obtaining increment density measurements along the entire otolith radius are important, and should not be done at random.

Despite the utility of the technique of age estimation developed, potential biases in size range and number of otoliths sampled make it difficult to compare growth estimates for *Etelis carbunculus* quantitatively. Results presented imply that a more systematic sampling program may document significant regional differences in growth and population dynamics of this species. The relationship between otolith growth rate and postrostral radius was similar for all regions. However, there were regional differences in the width of otoliths for a given fork length (Appendix 1), wider otoliths being found in Hawaii and French Polynesia. Although there were few fish sampled from Vanuatu and limited overlap occurs with small organisms from the other regions, fish from NMI and Vanuatu had smaller otolith radius (lower estimated age) than fish of similar size from the other two areas. This means that even if growth rates of otoliths were essentially equal throughout the Pacific, fish would be older at a given fork length in Hawaii and French Polynesia. Thus, well below the forced values of asymptotic length used in regressions, regional differences in estimated age are apparent.

Fish apparently grow faster at Vanuatu and NMI than in any of the other regions. However, at NMI they reach less than half the size found in the region near Vanuatu. This suggests there are differences in natural mortality rates for these regions (asymptotic length estimates were obtained from virgin stocks for NMI and in the initial stage of the fishery at Vanuatu). The growth curves for NMI yielded higher estimates of the von Bertalanffy growth constant (K) and, as a result, natural mortality estimates were higher. The differences in K hold true even for the NMI regression that was constrained only in t_0, but as mentioned the results from NMI should be interpreted with caution. Hawaii and French Polynesia showed similar values of K to Vanuatu, but fish from these regions had thicker otoliths and were apparently more slow growing. Possible explanations for such differences include genetic differences in regional stocks, variation in the mean annual temperature, and differences in feeding or food availability.

The estimates of the von Bertalanffy growth curve were in the range of those obtained in previous studies. Although Uchida et al. (1982) estimated K at 0.36 for the Hawaiian Islands, Ralston and Kawamoto (1987) obtained values of 0.15–0.17, which is more consistent with the present results. Both Uchida et al. (1982) and Ralston and Kawamoto (1987) based their estimates on length-frequency data from exploited stocks. Ralston and Williams (1988b) estimated K for virgin stocks at NMI from 0.13 to 0.35, depending on the method used. K estimates from commercial landings data at the onset of the fishery at Vanuatu were in the range 0.07–0.19 (Brouard et al. 1983, Brouard and Grandperrin 1985). Thus, the present K estimates seem reasonable. Estimates of t_0 were considerably greater than zero, except in the case of NMI, which was almost certainly a function of the limited number of small fish included in the data.

The similarity of otolith growth rate at any given radial distance was pointed out by Ralston and Miyamoto (1983), but these authors did not discuss the implications with regard to otolith shape for fish with different growth rates. The similarity of growth rate of otoliths and regional variation in growth rate of fish may explain some regional differences in otolith shape. It also indicates that there are species-specific characteristics of otolith growth from one region to another, as would be expected. If the concept of narrower or thinner otoliths corresponding to faster-growing organisms within a given species can be generally applied to fishes, then this is a tool that can be useful for a number of purposes (for example, in evaluating paleontological evidence of growth rates in sedimentary strata). Although environmental and genetic components of otolith shape must also be considered, differences in growth rate may explain many of the differences in shape which have commonly been used to separate the otoliths of different stocks, or "races," of the same species (Postuma and Zijlstra 1958, Parrish and Sharman 1959, Kotthaus 1961, Messieh 1972, Bird et al. 1986). Variation in growth may also explain sex-linked differences in the thickness of otoliths of sexually dimorphic fishes (Gaemers and Crapon de Crapona 1986). The present study is a contribution to the development of methodology that will be useful in evaluating these and other questions regarding the growth rate and shape of otoliths.

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Citations

Atkinson, K.E.
1989 An introduction to numerical analysis. John Wiley, NY, 693 p.

Barkman, R.C.
1978 The use of otolith growth rings to age young Atlantic silversides, *Menidia menidia*. Trans. Am. Fish. Soc. 107(6): 790–792.

Bird, J.L., D.T. Eppler, and D.M. Checkley Jr.
1986 Comparison of herring otoliths using Fourier series shape analysis. Can. J. Fish. Aquat. Sci. 43:1228–1234.

Brothers, E.B., C.P. Mathews, and R. Lasker
1976 Daily growth increments in otoliths from larval and adult fishes. Fish. Bull., U.S. 74:1–8.

Brouard, F., and R. Grandperrin
1985 Deep-bottom fishes of the outer reef slope in Vanuatu. *In* 17th Regional Technical Meeting on Fisheries, South Pacific Comm., ORSTOM, New Caledonia, [Engl. transl.], 127 p.

Brouard, F., R. Grandperrin, M. Kulbicki, and J. Rivaton
1983 Note on readings of daily increments observed on the otoliths of deepwater demersal fishes at Vanuatu. ORSTOM Notes et Documents d'Oceanographie 8, 9 p. [Transl. 88, W.G. Van Campen, avail. Honolulu Lab., NMFS, Southwest Fish. Sci. Cent.]

Carlot, A.H., and F. Nguyen
1989 Preliminary study on population dynamics of Vanuatu deep bottom fish after seven years of exploitation,. Paper presented at Tropical Fisheries Resource Assessment Workshop, sponsored by US AID–National Marine Fisheries Service–University of Hawaii, Manoa, July 5–26, 1989, 23 p. Avail. Fish. Dep., Port Vila, Vanuatu.

Davies, N.M., R.W. Gauldie, S.A. Crane, and R.K. Thompson
1988 Otolith ultrastructure of smooth oreo, *Pseudocyttus maculatus*, and black oreo, *Allocyttus* sp., species. Fish. Bull., U.S. 86:499–515.

Davis, P., and P. Rabinowitz
1984 Methods of numerical integration, 2d ed. Academic Press, NY, 612 p.

Gaemers, P.A.M., and M.D. Crapon de Crapona
1986 Sexual dimorphism in otoliths of haplochromines (Pisces, Cichlidae). Ann. Mus. R. Afr. Cent. Sc. Zool. 251:151–155.

Gaschütz, G., D. Pauly, and N. David
1988 A versatile BASIC program for fitting weight and seasonally oscillating length growth data. Int. Counc. Explor. Sea, CM 1980/D:6 Statistics Committee, 23 p.

Gauldie, R.W., I.F. West, and N.M. Davies
1989 K-selection characteristics of orange roughy (*Hoplostethus atlanticus*) stocks in New Zealand waters. J. Appl. Ichthyol. 5:127–140.

Geffen, A.J.
1986 The growth of herring larvae, *Clupea harengus* L., in the Clyde: An assessment of the suitability of otolith ageing methods. J. Fish Biol. 28:279–288.

Gompertz, B.
1825 On the nature of the function expressive of the law of human mortality, and on a new method of determining the value of life contingencies. Philos. Trans. R. Soc. Lond. 513–585.

Jones, C.
1986 Determining age of larval fish with the otolith increment technique. Fish. Bull., U.S. 84:91–103.

Jones, C., and E.B. Brothers
1987 Validation of the otolith increment ageing technique for striped bass, *Morone saxatilis*, larvae reared under suboptimal feeding conditions. Fish. Bull., U.S. 85:171–178.

Kotthaus, A.
1961 Preliminary remarks about redfish otoliths. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 150:45–50.

Manooch, C.S. III
1987 Age and growth of snappers and groupers. *In* Polovina, J.J., and S. Ralston (eds.), Tropical snappers and groupers: Biology and fisheries management, p. 329–373. Westview Press, Boulder, CO.

McGurk, M.D.
1984 Ring deposition in the otoliths of larval Pacific herring *Clupea harengus pallasi*. Fish. Bull., U.S. 82:113–120.

Messieh, S.N.
1972 Use of otoliths in identifying herring stocks in the southern Gulf of St. Lawrence and adjacent waters. J. Fish. Res. Board Can. 29:1113–1118.

Methot, R.D. Jr.
1981 Spatial covariation of daily growth rates of larval northern anchovy, *Engraulis mordax*, and the northern lampfish, *Stenobrachius leucopsarus*. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 178:424–431.
1983 Seasonal variation in survival of larval northern anchovy, *Engraulis mordax*, estimated from the age distribution of juveniles. Fish. Bull., U.S. 81:741–750.

Neilson, J.D., G.H. Geen, and D. Bottom
1985 Estuarine growth of of juvenile chinook salmon (*Oncorhynchus tshawytcha*) as inferred from otolith microstructure. Can. J. Fish. Aquat. Sci. 42:899–909.

Pannella, G.
1971 Fish otoliths: Daily growth layers and periodical patterns. Science (Wash. DC) 173:1124–1127.
1974 Otolith growth patterns: An aid in age determination in temperate and tropical fishes. *In* Bagenal, T.B. (ed.), The ageing of fish, p. 28–39. Unwin Bros., Surrey, England.

Parrish, B.B., and D.P. Sharman
1959 Otolith types among summer-autumn spawning herring in the Northern North Sea. J. Cons. Perm. Int. Explor. Mer 25:81–92.

Postuma, K.H., and J.J. Zijlstra

1958 On the distinction between herring races in autumn and winter spawners in the North Sea and English Channel by means of otoliths and the application of this method in tracing offspring of races along the continental coast. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 143(2):130-133.

Radtke, R.L.

1987 Age and growth information available from the otoliths of the Hawaiian snapper, *Pristipomoides filamentosus*. Coral Reefs 6:19–25.

Ralston, S.

1976 Age determination of a tropical reef butterflyfish utilizing daily growth rings of otoliths. Fish. Bull., U.S. 74: 990–994.

1981 A study of the Hawaiian deepsea handline fishery with special reference to the population dynamics of opakapaka, *Pristipomoides filamentosus* (Pisces: Lutjanidae). Doctoral diss., Coll. Fish., Univ. Wash., Seattle, 204 p.

1985 A novel approach to aging tropical fish. ICLARM (Int. Cent. Living Aquat. Resour. Manage.) Newsletter 8(1):14–15.

1987 Mortality rates of snappers and groupers. *In* Polovina, J.J., and S. Ralston (eds.), Tropical snappers and groupers: Biology and fisheries management, p. 375–404. Westview Press, Boulder, CO.

Ralston, S., and K. Kawamoto

1987 An assessment and description of the status of bottom fish stocks in Hawaii. Admin. Rep. H-87-7, NMFS Southwest Fish. Sci. Cent., Tiburon, CA, 55 p.

Ralston, S., and G.T. Miyamoto

1981 Estimation of the age of a tropical reef fish using the density of daily growth increments. *In* Gomez, E.D., et al. (eds.), The reef and man; Proc., 4th Int. Coral Reef Symp., Mar. Sci Cent., Univ. Philippines, Manila, vol. 1, p. 83–88.

1983 Analyzing the width of daily otolith increments to age the Hawaiian snapper, *Pristipomoides filamentosus*. Fish. Bull., U.S. 81:523–535.

Ralston, S., and H.A. Williams

1988a Numerical integration of daily growth increments: An efficient means of ageing tropical fishes for stock assessment. Fish. Bull., U.S. 87:1–16.

1988b Depth distributions, growth, and mortality of deep slope fishes from the Mariana Archipelago. U.S. NOAA-TM-NMFS-SWFC Tech. Memo. 113, NMFS Southwest Fish. Sci. Cent., Tiburon, CA, 47 p.

Ricker, W.E.

1973 Linear regressions in fishery. J. Fish. Res. Board Can. 30:409–434.

Salas, S.L., E. Hille, and J.T. Anderson

1986 Calculus, 5th ed. John Wiley, NY, 719 p.

SAS (Statistical Analysis System)

1985 Version 6. A series of user's manuals, statistical procedures and software for the personal computer. SAS Inst. Inc., Cary, NC.

Struhsaker, P., and J.H. Uchiyama

1976 Age and growth of the nehu, *Stolephorus purpureus* (Pisces: Engraulidae), from the Hawaiian Islands as indicated by daily growth increments of sagittae. Fish. Bull., U.S. 74:9–17.

Uchida, R.N., D.T. Tagami, and J.H. Uchiyama

1982 Results of bottom fish research in the northwestern Hawaiian Islands. Admin Rep. H-82-10, Honolulu Lab., Southwest Fish. Sci. Cent., 15 p.

von Bertalanffy, L.

1957 Quantitative laws in metabolism and growth. Q. Rev. Biol. 32:217–231.

Wall, H.S.

1948 Analytic theory of continued fractions. D. Van Nostrand, NY, 433 p.

Wild, A., and T.J. Foreman

1980 The relationship between otolith increments and time for yellowfin and skipjack tuna marked with tetracycline. Inter-Am. Trop. Tuna Comm. Bull. 17:557–590.

Winsor, C.P.

1932 The Gompertz curve as a growth curve. Proc. Natl. Acad. Sci. 18(1):1–8.

Wrobel, L.

1985 La peche profonde en Polynesie Francaise. Etablissement pour la valorisation des activites aquacoles et maritimes (EVAAM), Minist. de la Mer, French Polynesia, 81 p.

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Mean circulation and variability on the eastern Canadian continental shelf

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Abstract—The circulation and variability on eastern Canadian continental shelves is reviewed with emphasis on horizontal and vertical structure in the water column. Mean and seasonal currents, sheared by stratification and friction, generally follow bathymetry and are driven primarily by surface wind stress and buoyancy fluxes. In certain near-resonant embayments, nonlinear interactions of the tide also make significant contributions to the mean and low-frequency currents. Direct forcing of low-frequency shelf circulation by offshore currents and pressure fields is of lesser importance according to recent observations and models. At higher frequencies, the wintertime response to atmospheric forcing occurs in three important frequency bands: surface wave (periods of 2–20 s), inertial (17–22 h) and synoptic or subtidal (2–10 days). Most of the subtidal energy in the subsurface pressure (SSP) field is attributable to direct local forcing by alongshore wind and to remote forcing by coastal-trapped waves (CTW). The subtidal current variability is less coherent with these sources primarily because of small scale circulations created by vortex stretching, topographic steering and scattering by the rugged shelf bathymetry. Bottom friction and scattering control the ratio of locally and remotely forced subtidal energy as a function of position on the shelf. Intermittent inertial currents in stratified shelf waters, often associated with mesoscale atmospheric forcing, exhibit a 180° phase change across the pycnocline and are inhibited near the coast. Surface waves generated by storm winds are strongly dissipated in shallow water, where they enhance bottom stresses that: (1) balance the surface wind stress; and (2) may contribute to the damping of inertial waves. Specific examples of these phenomena are drawn from observations on the Scotian Shelf and in the Gulf of Maine.

INTRODUCTION

THE continental margin of eastern Canada is characterized by broad shelves (100–200 km) with rugged topography, separated from the abyssal depths by a steep continental slope. Deep basins and marginal troughs (>200 m) are typically found in the nearshore regions of the shelf, whereas long chains of shallow banks in the offshore regions often create a natural barrier to exchanges between oceanic and coastal waters. The coastline is also quite irregular, punctuated by several large gulfs and embayments (for example Gulf of Maine, Gulf of St Lawrence, Hudson Strait; Fig. 1a). All of these physical features have important consequences for the structure and variability of the coastal circulation.

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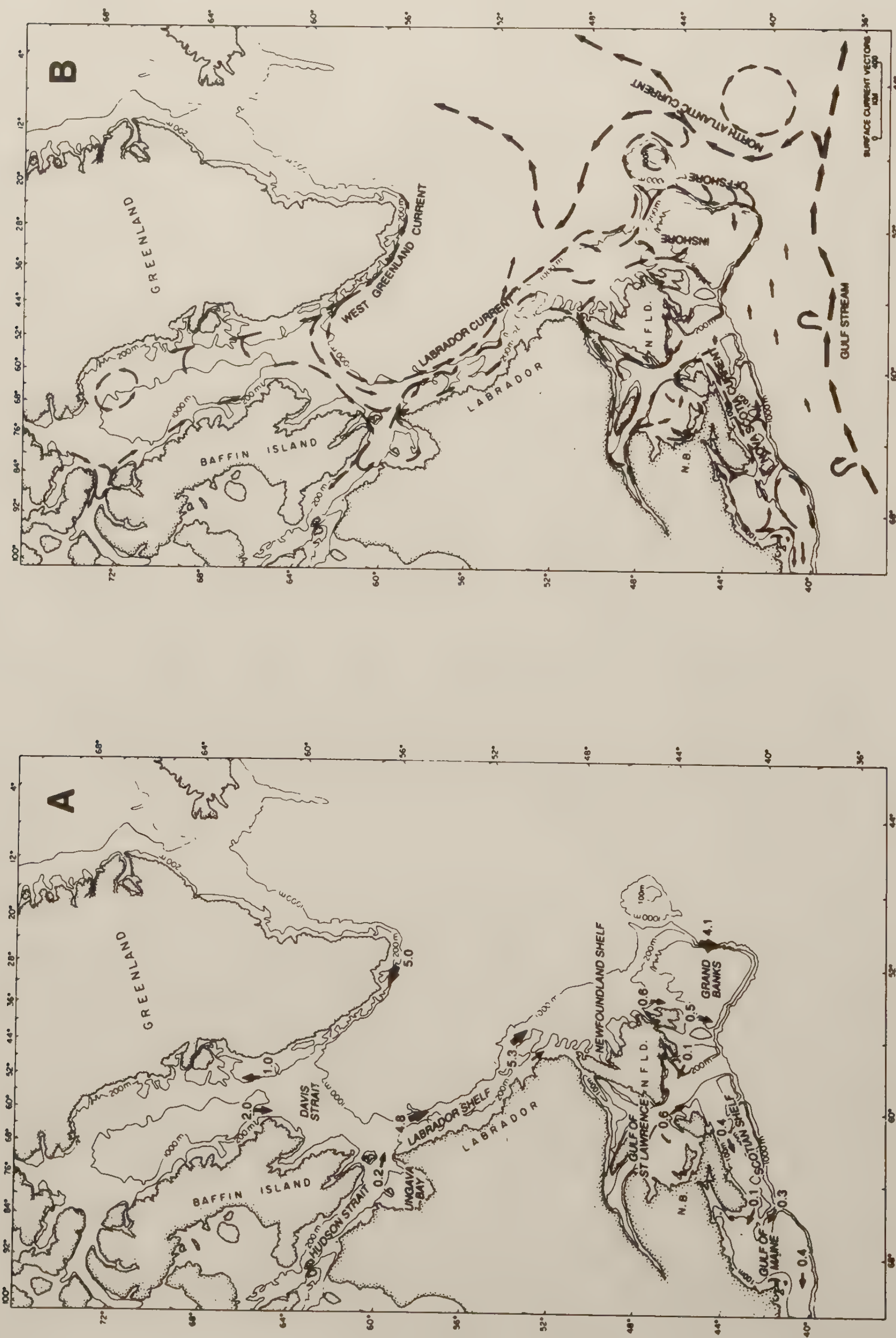
B
GREENLAND
BAFFIN ISLAND
LABRADOR
WEST GREENLAND CURRENT
LABRADOR CURRENT
NORTH ATLANTIC CURRENT
OFFSHORE
INSHORE
NFLD.
N.B.
NOVA SCOTIA CURRENT
GULF STREAM
SURFACE CURRENT VECTORS
200m
1000m
A
GREENLAND
BAFFIN ISLAND
DAVIS STRAIT
HUDSON STRAIT
UNGAVA BAY
LABRADOR SHELF
LABRADOR
NEWFOUNDLAND SHELF
GULF OF ST LAWRENCE
NFLD.
GRAND BANKS
SCOTIAN SHELF
N.B.
GULF OF MAINE
5.0
1.0
2.0
0.2
4.8
5.3
0.6
0.5
4.1
0.1
0.6
0.4
0.1
0.3
0.4
200m
1000m

Potentially important driving forces for the coastal circulation include the surface wind stress, tidal forces, buoyancy fluxes and the large-scale circulation associated with adjacent deep ocean gyres. Wind stress influences the flow on a wide range of time scales from the steady mean currents to the order of seconds for surface gravity waves. In winter, wind-driven circulation often dominates in two frequency bands: (1) the synoptic band (periods of 2–10 days) associated with severe storms; and (2) the inertial band (periods of 17–22 h; Smith *et al.*, 1978). Surface gravity waves generated by winter storms also have a significant effect on the low-frequency circulation (and the seabed) in shallow water through their enhancement of bottom shear stress (Grant and Madsen, 1979). However, in southern regions such as the Scotian Shelf, the mean wind stress (eastward) opposes the mean shelf current (southwest). This fact led Csanady (1976) to conclude that an alongshore pressure gradient of some other origin must drive the mean flow. But recent studies (Brink, 1986; Haidvogel and Brink, 1986) suggest that rectification of wind-driven current fluctuations by topographic drag asymmetries may contribute to the mean flow in the direction of CTW propagation (southwest).

Buoyancy fluxes associated with large freshwater inputs to the coastal zone produce strong density gradients leading to alongshore pressure gradients that drive alongshore current (Csanady, 1976; 1978). Baroclinicity can also interact with shelf–slope topography through the so-called JEBAR effect (Joint Effect of Baroclinicity and Relief; Shaw and Csanady, 1983; Huthnance, 1984; Weaver and Hsieh, 1987) to induce depth-averaged advection on the shelf. These mechanisms generally operate at very long time scales (seasonal or greater), consistent with the freshwater forcing cycles.

Offshore forcing has also been proposed as the origin of the alongshore pressure gradient that drives the mean flow on the shelf. Beardsley and Winant (1979) concluded that local buoyancy fluxes were insufficient forcing on the U.S. east coast and that the required pressure gradient originates as a boundary effect of the large-scale circulation. However, more recent studies (Wang, 1982; Csanady and Shaw, 1983) have used barotropic models to demonstrate the "insulating" effect of the continental slope which traps the effects of large-scale pressure gradients over the upper slope and prevents them from penetrating onto the shelf. Furthermore, results of a stratified steady model (Kelly and Chapman, 1988) have shown that the effects of reasonable stratification and vertical structure of the imposed pressure field are unable to break this topographic constraint, although they do have a significant impact on the distribution of energy over the slope.

On a smaller scale, offshore eddies and rings have an important influence on the circulation over the slope and rise. Gulf Stream warm-core rings, for example, entrain large quantities of coastal water from the Scotian Shelf (Smith, 1978), while interactions between the Labrador Current and eddies of the North Atlantic Current system are probably responsible for the high rate of loss of surface drifters along the southeastern flank of the Grand Banks of Newfoundland (Petrie and Anderson, 1983; Greenberg and Petrie, 1988). When a Gulf Stream ring suddenly encounters a sloping bottom, it radiates low-frequency energy in the form of topographic Rossby waves with characteristic periods

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Fig. 1. (A) Estimates of volume transport on the continental shelf off eastern Canada. Numbers represent transport in units of 10^6 m^3 s^{-1} (after Chapman and Beardsley, 1989). (B) Qualitative estimation of the surface circulation off eastern Canada (see Greenberg and Petrie, 1988).

of 10–30 days (LOUIS and SMITH, 1982; LOUIS *et al.*, 1982). On approach to the shelf, however, the wave energy is strongly refracted by the continental slope and scattered into baroclinic modes trapped to the shelf edge such that little energy penetrates onto the shelf (SMITH, 1983a). Furthermore, frictional dissipation limits the influence of the waves on the shelf circulation. CHAPMAN and BRINK (1987) have used a linear, stratified model to examine the shelf and slope circulations induced by periodic offshore forcing and conclude that, at the energetic deep ocean time scales (periods greater than 10 days), the shelf response is inevitably weak and barotropic. In addition, the response to a single translating eddy (with realistic vertical structure) moving close to the slope is blocked by the topography and "squashed" at the shelf break. Only a very weak circulation cell is induced over the shelf. Thus, the consensus appears to be that offshore forcing does not have an important influence on the general circulation of the shelf at low frequencies. Nevertheless, eddies do affect near-bottom currents, stress and sediment transport near the shelf break, i.e. at depths of 200–400 m (BUTMAN, 1987).

The dynamics of the "first-order" barotropic tidal circulation on the continental shelf are reasonably well understood through the calibration and verification of numerical models (e.g. PETRIE *et al.*, 1987a). Furthermore, geometries such as the Gulf of Maine/Bay of Fundy (GREENBERG, 1983) and Ungava Bay (GRIFFITHS *et al.*, 1981) produce near-resonant responses at semidiurnal frequencies such that: (1) tidal currents dominate local kinetic energy budgets; and (2) significant residual mean, monthly, fortnightly and higher harmonic (shallow water tidal) circulations develop through nonlinear interaction (LODER, 1980). In shallow regions, such as Georges Bank and the inner Bay of Fundy, the tidal currents vertically mix the water column and largely govern the resuspension of bottom sediment (BUTMAN, 1987; AMOS and JUDGE, this issue). Under these conditions, barotropic models permit reasonable simulations of sediment transport and deposition (GREENBERG and AMOS, 1983).

On the other hand, the dynamics of the tidally-induced residual flow field in deeper areas are not well known, nor are the flows themselves easily determined by observations (TEE *et al.*, 1988). Furthermore, in order to model shelf circulation processes properly, the rates of dissipation and mixing of momentum and density must be accurately specified. For example, WRIGHT and LODER (1988) have shown that model estimates of topographic rectification of tidal currents are sensitive to the parameterization scheme for bottom friction. This uncertainty frustrates attempts to compare model results to observations. Similarly, spatial variations in the strength of a linear bottom friction coefficient can have a significant impact on the structure of the wind-driven response (CLARKE and BRINK, 1985) or on the downstream evolution of the barotropic mean flow on the shelf (CHAPMAN *et al.*, 1986).

This review will be focused on recent advances in understanding certain aspects of the circulation on the continental shelves of Atlantic Canada. Some simple, linear, barotropic models are first examined. The mean and seasonal circulation patterns will then be presented followed by a description of wind-driven variability. Emphasis throughout will be placed on the vertical and horizontal structure of flow fields. The direct effects of offshore forcing will not be considered further because of its generally weak influence on the shelf circulation. Moreover, in spite of their dominance in some regimes, tidal currents will be largely ignored. Finally, though the physical processes discussed are generally found over the entire eastern shelf region, specific examples are drawn primarily from two experiments conducted on the Scotian Shelf: the Cape Sable Experiment, 1979–1980

(SMITH, 1983b) and the Canadian Atlantic Storms Program (CASP, December 1985–April 1986; ANDERSON and SMITH, 1989).

SIMPLE DYNAMICAL MODELS

From the wealth of recent observations, a number of important concepts have emerged to explain the primary dynamical balances in the mean and low-frequency circulation of the coastal ocean (CSANADY, 1982). Following WRIGHT (1986), the linearized, shallow water hydrodynamic equations may be derived under the assumptions that the homogeneous fluid layer is thin (hydrostatic) and that weak velocities render the convective accelerations much smaller than the Coriolis terms:

$$u_t - fv = -g\zeta_x - \frac{ru}{h}, \tag{1}$$

$$v_t + fu = -g\zeta_y - \frac{rv}{h} + \frac{\tau^y}{\rho h}, \tag{2}$$

$$(hu)_x + (hv)_y = \zeta_t, \tag{3}$$

where the subscripts denote differentiation, (u, v) are the depth-averaged horizontal velocity components in the x (cross-shore) and y (alongshore) directions, $z = -h(x, y)$ is the bottom and $z = \zeta(x, y, t)$ is the position of the sea surface. The flow is forced by the alongshore wind stress component, $\tau^y(x, y, t)$, and retarded by linear bottom friction,

$$\text{bottom stress} = \rho(ru, rv) \tag{4}$$

where $r(x, y)$ is a spatially-varying resistance coefficient.

For harmonic time dependence $[\zeta(x, y, t) = Re(\bar{\zeta}(x, y)e^{-i\omega t})]$, (1)–(3) may be reduced to a single equation

$$-h_x\bar{\zeta}_y + h_y\bar{\zeta}_x = f^{-1}[(r - i\omega h)\bar{\zeta}_x]_x \tag{5}$$

with the coastal boundary condition of no normal transport

$$h\bar{\zeta}_y + f^{-1}(r - i\omega h)\bar{\zeta}_x = \frac{\bar{\tau}^y}{\rho g} \qquad \text{at } x = 0 \tag{6}$$

under the following reasonable assumptions for the shelf setting

$$(\omega/f)^2 \ll 1 \qquad \text{low frequency} \tag{7a}$$

$$(r/fh)^2 \ll 1 \qquad \text{weak friction} \tag{7b}$$

$$(L_x/L_y)^2 \ll 1 \qquad \text{long wave approximation} \tag{7c}$$

$$(L_x/\lambda_e)^2 \ll 1 \qquad \text{rigid lid} \tag{7d}$$

$$L_x/L_\tau \ll 1 \qquad \text{uniform forcing} \tag{7e}$$

where L_x, L_y are the scales of variation in the cross-shelf and alongshore directions, $\lambda_e = \sqrt{gh}/f$ is the external Rossby deformation scale and L_τ is the scale for variations in the wind field. With certain further simplifications, equations (5) and (6) have spawned a number of illustrative models whose basic character is dictated by the parameter, $r/\omega h$, the ratio of the forcing time scale (ω^{-1}) to the frictional spindown time (h/r).

The quasisteady limit ($r/\omega h \gg 1$) with plane beach topography [$h = h(x)$, $h_x = s =$ constant] and constant r leads to CSANADY's (1978, 1981) "arrested topographic wave" (ATW) solutions. Two canonical solutions for such an idealized shelf region are obtained by analogy with one-dimensional heat conduction. First of all, in the absence of wind ($\tau^y = 0$), the pressure field resulting from a coastal mass source applied at a particular cross-shelf transect (the "backward boundary")

$$\bar{\zeta} = \zeta_o(x) = M\delta(x) \qquad \text{at } y = 0 \tag{8}$$

"diffuses" away from the coast for increasing values of the time-like variable, $-y$. The solutions for sea level and depth-averaged alongshore current are given by (CSANADY, 1981)

$$\bar{\zeta}_Q(x, y) = \left(\frac{2}{\pi}\right)^{1/2} \frac{M}{L_x} e^{-\xi^2} \tag{9a}$$

$$\bar{v}_Q(x, y) = -\frac{2}{\pi^{1/2}}\left(\frac{fQ}{2ry}\right) \xi e^{-\xi^2} \tag{9b}$$

where

$$L_x = (-2ry/fs)^{1/2} \tag{10}$$

is the cross-shelf scale of the coastal boundary layer, $\xi = x/2^{1/2}L_x$, and $Q = -gsM/f$ is the volumetric alongshore transport. The effective diffusivity is r/fs and, because of the parabolic nature of the equation, the distribution imposed at $y = 0$ affects the shelf circulation only in the "forward" direction ($y < 0$) in the sense of shelf wave propagation.

On the other hand, when the boundary forcing is absent [$\zeta = \zeta_o(x) = 0$ at $y = 0$], the solution for steady wind forcing over a limited portion of the shelf

$$\frac{\tau^y}{\rho} = \begin{cases} F, & y < 0 \\ 0, & y > 0 \end{cases} \tag{11}$$

is given by (CSANADY, 1978)

$$\bar{\zeta}_W = -\left(\frac{2}{\pi}\right)^{1/2} \frac{fF}{rg} L_x\{e^{-\xi^2} - \pi^{1/2}\xi erfc(\xi)\} \tag{12a}$$

$$\bar{v}_W = \frac{F}{r} erfc(\xi). \tag{12b}$$

Again a coastal boundary layer of scale, L_x, grows in the $y < 0$ direction as it absorbs or emits the cross-shelf Ekman flux associated with the alongshore wind.

The normalized cross-shelf profiles of depth-averaged alongshore current are plotted in Fig. 2a as a function of the scaled variable, $\xi(x, y) = x/2^{1/2}L_x(y)$. The boundary-driven current vanishes at the coast along with ζ_x and achieves a maximum value at $x = L_x$. Close to shore, the alongshore gradient, ζ_y, drives the flow against friction, while offshore ($x > L_x$), the gradient changes sign as the Coriolis force of the cross-shore transport becomes important. In contrast, the wind-forced current is maximum at the coast, where

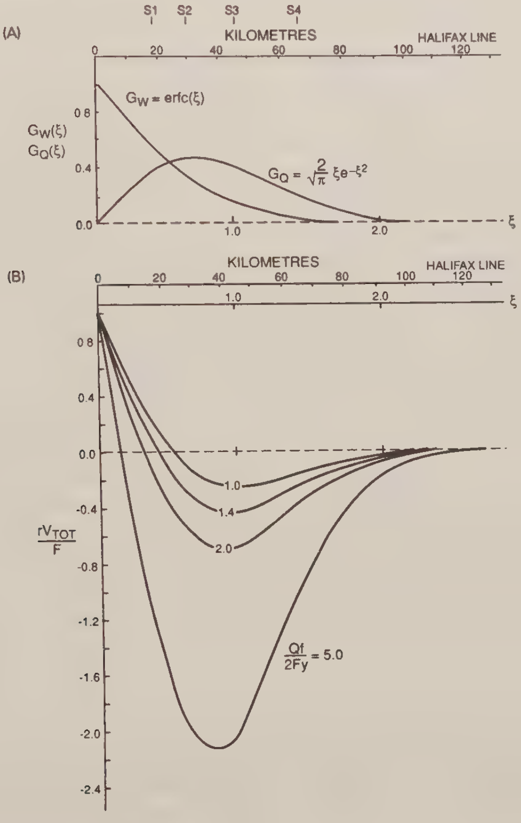


Fig. 2. (A) Cross-shelf structure functions for alongshore velocity from the frictional barotropic models on a plane beach: $G_W(\xi)$ for the local wind-forced solution (12b) and $G_Q(\xi)$ for the boundary-forced solution (9b). (B) Scaled distribution for the cross-shelf profile of alongshore current as a function of downshelf distance in the forward direction.

surface and bottom stresses balance as $h \Rightarrow 0$, and decreases monotonically in the offshore direction.

On a typical east coast shelf, the mean flow is subject to both wind and boundary forcing. By virtue of linearity, the solutions (9) and (12) may be added to give an estimate of the combined alongshore flow resulting from the two forcings

$$\bar{v}_{\mathrm{TOT}} = \bar{v}_W + \bar{v}_Q = \frac{F}{r}\, erfc(\xi) - \frac{2}{\pi^{1/2}}\left(\frac{fQ}{2ry}\right)\xi e^{-\xi^2} = \frac{F}{r}[G_W(\xi) - KG_Q(\xi)] \qquad (13)$$

where $G_W(\xi) = erfc(\xi)$, $G_Q(\xi) = 2/\pi^{1/2}\xi e^{-\xi^2}$ and $K = fQ/2Fy$. For constant Q and F of opposite sign, the value of K, representing the relative influence of the boundary-forced flow, diminishes with increasingly negative y (Fig. 2b). This results in a nearshore flow reversal which migrates offshore within the scaled boundary layer structure. Of course, by virtue of that scaling, the streamlines are also migrating offshore as $(-y)^{1/2}$.

Wang (1982) solved numerically a somewhat more complicated steady problem with a segmented shelf/slope topography, offshore forcing ($\zeta_y = \gamma =$ constant at $x = W$) and alongshore depth variation [$h = h(x, y)$] to demonstrate the insulating effect of the continental slope and the channelling effect it has on the alongshore flow. Chapman *et al.* (1986) used a similar model with weaker variable friction [$r = r(x)$] to demonstrate that the unusually rapid shift of Wang's coastal current to the slope region was a consequence of his specification of a large, constant value of r. In another paper, Chapman (1986) also demonstrates that the cross-shelf convergence associated with shelf/slope topography and variable friction is capable of maintaining a front in the distribution of a passive tracer near the shelf break. Wright (1989) then showed that a similar mechanism operates even when there is a significant density contrast across the front; that is, friction will cause the front to migrate across the shelf region, then "stall" in the vicinity of the shelf break.

In the very weak friction limit ($r/\omega h \ll 1$), equations (5) and (6) result in damped Rossby waves either locally forced or propagating into the domain as free waves from the backward boundary (Gill and Schumann, 1974). Weak friction acts to damp the free wave amplitudes in the forward direction and produce phase shifts between the nearshore and offshore fluctuations, whereas for forced waves, the phase difference between the stress and velocity is reduced by friction (Brink and Allen, 1978; Wright, 1986).

For constant r and frequency, ω, the parameter $r/\omega h$ increases shoreward on a constant sloping bottom. Comparing the zone where $r/\omega h \gg 1$ with the ATW trapping zone, $x < L$, Wright (1986) concluded that arrested topographic wave dynamics are strictly applicable only at very low frequencies,

$$\omega / f \ll rl/2h_x\omega \cong 10^{-2}$$

where l is the wave number for periodic forcing. However Schwing (1989a) has demonstrated that the time-dependent ATW solution (ATW spatial pattern with harmonic time dependence) is useful at much higher frequencies, well into the wind forced band.

MEAN AND SEASONAL CIRCULATION

Mean circulation

Chapman and Beardsley (1989) have suggested that the mean circulation off Canada's east coast is part of a 5000 km buoyancy-driven coastal current which originates off the southern coast of Greenland. They base this proposal on oxygen isotope data which show that the freshwater component of the shelf water as far south as the Middle Atlantic Bight (off the eastern U.S.) is highly depleted in ^{18}O. The isotopic content is similar to that of local glacial melt and river runoff into the northern Labrador Sea, suggesting that the associated buoyancy fluxes may be important driving forces for the coastal flow. This hypothesis is consistent with most of the known features of the mean circulation (Fig. 1). The measured (or inferred) transports and the estimated surface currents indicate that the dominant component of the flow follows the west coast of Greenland, then splits near the sill in Davis Strait with the southern branch feeding the flow onto the Labrador Shelf. The southward flow accelerates (to 0.4–0.6 m s^{-1}) as it passes Hudson Strait due to bathymetric convergence and the injection of additional freshwater (with roughly the same isotopic content) from Hudson Strait. The primary branch of the Labrador Current lies along the shelf break, but a significant alongshore current also follows the marginal trough (Piper, this issue). The complex bathymetry, with numerous channels and saddles, allows a liberal exchange to take place. Near 48°N, the inshore and offshore branches of the Labrador Current diverge with the offshore branch (90%) following the outer edge of the Grand Banks of Newfoundland while the inshore branch flows along the coast through Avalon Channel (PETRIE and ANDERSON, 1983). Some (20%) of the inshore branch then turns westward and enters the Gulf of St Lawrence while the rest flows offshore. Much of the offshore branch of the Current turns eastward at the southern tip of Grank Bank, but some continues westward as a deep "Labrador" component of the slope water off Nova Scotia (GATIEN, 1976).

Reinforced by freshwater runoff in the Gulf of St Lawrence, the coastal flow emanates from Cabot Strait into the nearshore region of the Scotian Shelf where it flows westward to the Gulf of Maine. Joining the deep slope water input through Northeast Channel, the coastal flow then exits the Gulf of Maine onto the New England Shelf. As on the Labrador Shelf, the rugged topography of the Scotian Shelf and Gulf of Maine strongly influences the path of the current and its exchange with offshore waters (SMITH *et al.*, 1978; HOUGHTON *et al.*, 1978). Some uncertainty surrounds the fate of the freshwater input to the Gulf of St Lawrence since its ^{18}O content should be quite distinct from that of the northern Labrador Sea, yet it is not detected in samples from the western Scotian Shelf or Gulf of Maine. Moreover, isotope data from the central Gulf of St Lawrence show little evidence of local runoff except in a thin surface layer (P. STRAIN, Chemical Oceanography, Bedford Institute of Oceanography, personal communication). CHAPMAN and BEARDSLEY (1989) attribute masking of the isotopic signature of the Gulf of St Lawrence runoff to thorough mixing with a much larger volume of Labrador water over the Scotian Shelf. This hypothesis requires testing.

Maximum mean surface velocities over the shelf (Fig. 1b) are generally associated with the major transports. In the West Greenland and offshore Labrador Currents speeds range from 0.4–0.6 m s^{-1}, while inshore currents in Avalon Channel and on the Scotian Shelf lie between 0.1 and 0.3 m s^{-1}.

Seasonal circulation

The hydrographic properties and longshore volume transport of coastal currents exhibit strong seasonal cycles as well as significant interannual variability which lead to inferences about freshwater sources and driving mechanisms. For instance, MYERS *et al.* (1989) have correlated seasonal salinity cycles (Fig. 3a) and residuals at Station 27 (off St Johns, Newfoundland) with similar variations in certain northern freshwater sources to demonstrate that Labrador sea ice-melt, not Hudson Bay runoff, is the primary determinant of the seasonal cycle in Newfoundland Shelf salinity, but that Hudson Bay residuals do impact its interannual variability.

Similarly SUTCLIFFE *et al.* (1976) and SMITH (1989b) have used seasonal cycles in temperature and salinity to infer that freshwater runoff into the Gulf of St Lawrence governs the seasonal but not the interannual variability on the Scotian Shelf. Moreover, DRINKWATER *et al.* (1979) and SMITH (1983b) have shown that the hydrographic cycles are associated with strong annual signals in alongshore transport. A comparison (Fig. 3b) of monthly mean transports in the Nova Scotian Current at Cabot Strait, Halifax and Cape Sable (off southwest Nova Scotia) reveals a distinct similarity when suitable lags (3 and 4 months, respectively) are applied to the Halifax and Cape Sable signals. These lags are

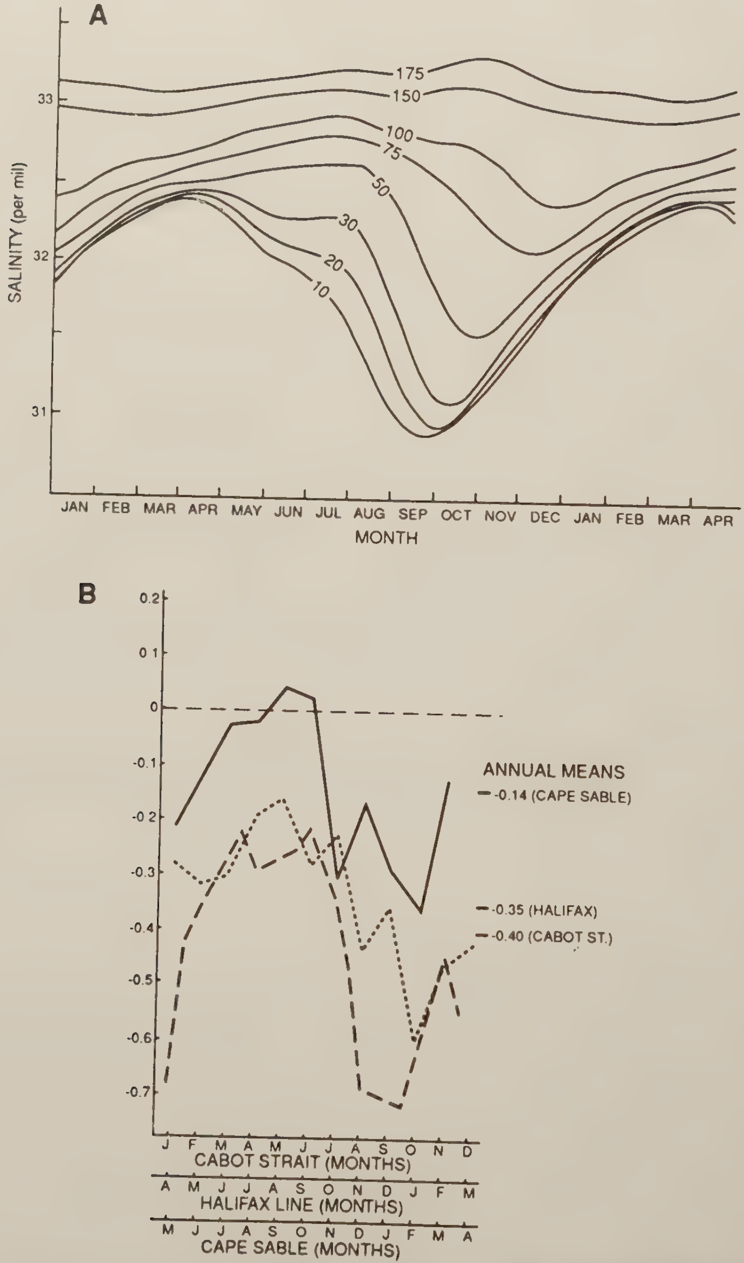


Fig. 3. (A) Seasonal salinity cycle at Station 27, off St Johns, Newfoundland, as a function of depth (from Myers *et al.*, 1989). (B) Monthly mean alongshore transports on the Scotian Shelf including geostrophic transports from Cabot Strait (dash) and the Halifax Section (dot) (both from Drinkwater *et al.*, 1979) and estimates from measured currents off Cape Sable (solid; Smith, 1983b). Note that different time scales suggest 3 and 4 month lags for the Halifax and Cape Sable signals behind Cabot Strait. Annual mean transports are indicated on the right.

consistent with alongshore advection at an average rate of 6 km day^{-1}. Note that the Cabot Strait and Halifax transports are based on geostrophic estimates, whereas the Cape Sable signal is calculated from measured mean currents. This may account, in part, for the large difference in the annual mean transport through the Cape Sable section. However, another possibility is the offshore migration of the axis of the Current because of friction and/or topographic steering.

Dynamics

Using a simple diagnostic model, SMITH (1983b) concluded from observations that the primary dynamical balance for the nearshore circulation on the western end of the Scotian Shelf involves alongshore gradients in pressure (i.e. sea level) and density as well as nonlinearities associated with topographic rectification of tidal currents (LODER, 1980). By imposing a 20 mm coastal setup (with a linear cross-shelf gradient to zero at the shelf break) on the eastern (backward) boundary, he was able to obtain reasonable agreement between observed depth-averaged annual mean currents and the M_2 tidal residual circulation of a nonlinear barotropic model (Fig. 4a). Prominent features produced by tidal rectification include a clockwise gyre over Browns Bank and an inshore jet off Cape Sable. The alongshore flow off Shelburne is due primarily to the alongshore pressure gradient set by the boundary condition.

Similarly, GREENBERG and PETRIE (1988) specified boundary forcing to be one half of the observed steric height profile along a Labrador Shelf transect in order to drive a barotropic model of the mean circulation on the Newfoundland Shelf and Slope (Fig. 4b). In spite of some obvious shortcomings, such as the absence of the Gulf Stream and North Atlantic Current, comparisons with observed depth-averaged currents show some quantitative agreement. However, some features, including the position and width of the Labrador Current and the observed clockwise gyre on Flemish Cap, are not reproduced and may be attributable to baroclinic effects.

Barotropic models have also been found useful in simulating the depth-averaged mean flow driven by wind. However, care must be taken to impose an appropriate condition at the backward boundary. For example, WRIGHT *et al.* (1986) specified a coastally-trapped pressure field equivalent to that of an arrested topographic wave (equation 12a) on their eastern boundary at Halifax in order to account for wind forcing over the portion of shelf not included in their model. Because the direct effects of the forcing over the domain are small near the backward boundary, the boundary forced component of flow is dominant over the western Scotian Shelf as suggested by Fig. 2b. Hence the depth-averaged model current (Fig. 5a) compared well with the observed mid-depth current responses only when the boundary forcing was applied (Fig. 5b).

In spite of the successes of the barotropic models in simulating observed depth-averaged currents, in many instances knowledge of the baroclinic structure of the flow is essential for determining certain aspects of the flow, for example, the transport of particulate matter near the surface or near the seabed. During the CASP experiment, volume transport on the Scotian Shelf attained its seasonal maximum in December 1985, then declined slowly until the end of the experiment in early April 1986 (ANDERSON and SMITH, 1989). The four-month mean currents (Fig. 6) show that along the 100 m isobath, the flow appears to be relatively barotropic, whereas in deeper water there is significant shear over the upper 100 m of the water column.

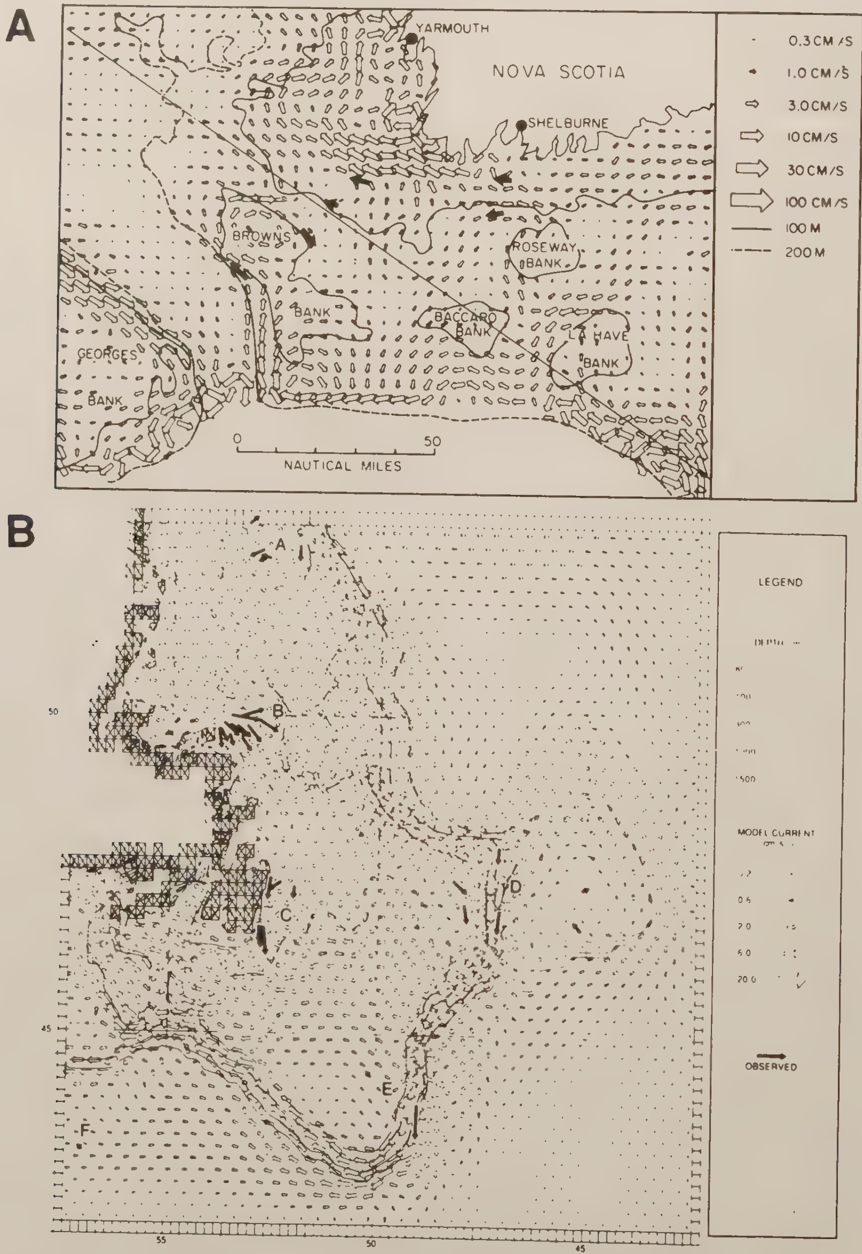

A
YARMOUTH
NOVA SCOTIA
SHELBURNE
BROWNS
BANK
ROSEWAY
BANK
BACCARO
BANK
LA HAVE
BANK
GEORGES
BANK
0
50
NAUTICAL MILES
0.3 CM/S
1.0 CM/S
3.0 CM/S
10 CM/S
30 CM/S
100 CM/S
100 M
200 M
B
A
B
C
D
E
F
50
45
55
50
45
LEGEND
DEPTH
MODEL CURRENT
OBSERVED

Fig. 4. Comparisons between the nonlinear, barotropic model and observations of the mean circulation. (A) Circulation in the eastern Gulf of Maine off Cape Sable, Nova Scotia. Measured currents (solid) are the depth-averaged annual means. Backward boundary of the model has been set up by 20 mm (see text; from Smith, 1983b). (B) Circulation on the Newfoundland Shelf. Measured currents (solid) are means from longest available records from the area. Backward boundary has been raised by an amount equal to one half the dynamic height on an historical hydrographic section on the Labrador Shelf. Arrow length is proportional to the square root of the current (after Greenberg and Petrie, 1988).

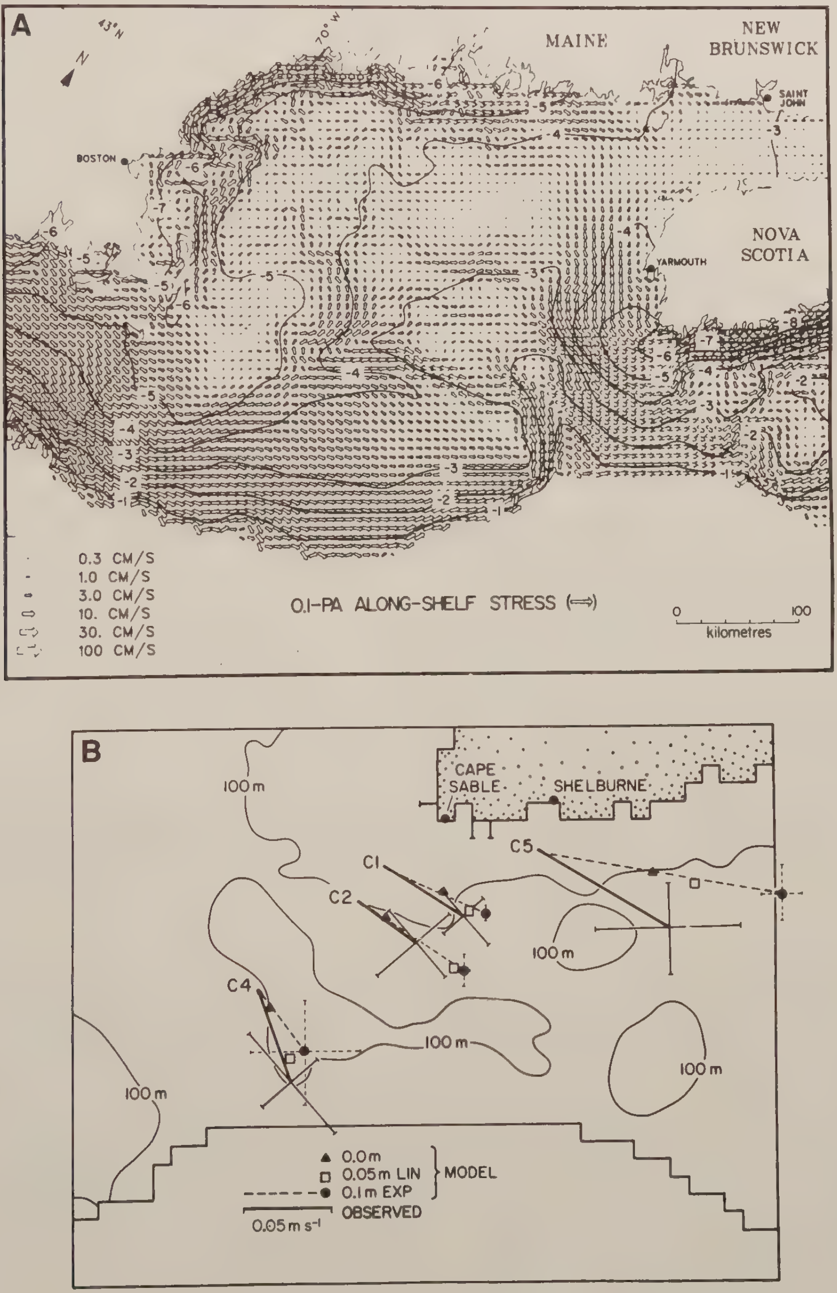

A
43°N
N
70°W
MAINE
NEW BRUNSWICK
SAINT JOHN
BOSTON
YARMOUTH
NOVA SCOTIA
0.3 CM/S
1.0 CM/S
3.0 CM/S
10. CM/S
30. CM/S
100 CM/S
0.1-PA ALONG-SHELF STRESS (⟹)
0
100
kilometres
B
CAPE SABLE
SHELBURNE
100 m
C1
C2
C4
C5
▲ 0.0 m
□ 0.05 m LIN
● 0.1 m EXP
MODEL
OBSERVED
0.05 m s⁻¹

Fig. 5. (A) Predicted elevations (cm) and currents from a linear barotropic model driven by a 0.1 Pa uniform alongshelf wind stress, including a 0.1 m exponential set-down across the backward boundary. (B) Comparison of model (dash) and observed (solid) current responses off southwest Nova Scotia for a 0.1 Pa alongshelf wind stress. Predicted responses include (▲) no set-up, (●) 0.1 m exponential set-up, and (□) 0.05 m linear set-up on the backward boundary (from WRIGHT *et al.*, 1986).

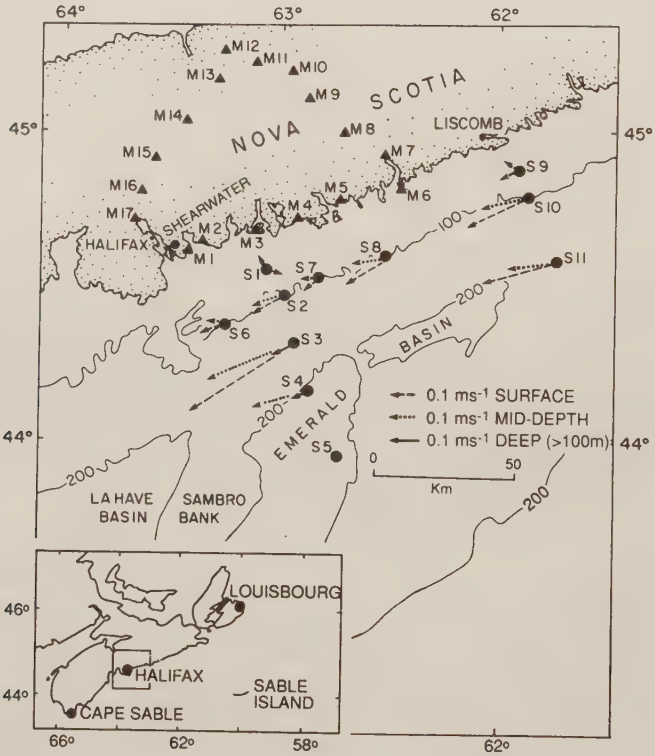

64°
63°
62°
45°
44°
NOVA SCOTIA
LISCOMB
SHEARWATER
HALIFAX
M1
M2
M3
M4
M5
M6
M7
M8
M9
M10
M11
M12
M13
M14
M15
M16
M17
S1
S2
S3
S4
S5
S6
S7
S8
S9
S10
S11
100
200
BASIN
EMERALD
LA HAVE BASIN
SAMBRO BANK
0.1 ms-1 SURFACE
0.1 ms-1 MID-DEPTH
0.1 ms-1 DEEP (>100m)
0
50
Km
46°
44°
66°
62°
58°
62°
LOUISBOURG
HALIFAX
SABLE ISLAND
CAPE SABLE

Fig. 6. Mean currents observed during the CASP field program (1 December 1985–31 March 1986) at moorings S1–S4 and S6–S11 from the surface layer (solid), mid-depth (40–100 m; dot) and deep layer (>100 m; dash). Mesoscale wind measurements were made at land-based mesonet stations (M1–M17) (from Anderson and Smith, 1989). Inset shows place names for the Scotian Shelf.

In a depth-averaged sense, the maximum current lies near S3 and S11 on the 150 m isobath, roughly 45 km from the coast, whereas the flow inshore on the 60 m isobath is much weaker and shows a tendency to reverse direction at S1 on the Halifax line. Using typical average parameters for this region of the Scotian Shelf ($f = 10^{-4}\ \mathrm{s}^{-1}$, $s = 3.5 \times 10^{-3}$, $r = 5 \times 10^{-4}\ \mathrm{m\ s}^{-1}$, $-y = 350$ km), the cross-shore scale length (10), $L_x \cong 32$ km, estimates the offshore position of the maximum depth-averaged alongshore current for the *boundary-forced* component of the flow. However, the mean alongshore stress during CASP ($\tau^y \cong 0.04$ Pa) implies $F = \tau^y/\rho = u_*^2 \cong 4 \times 10^{-5}\ \mathrm{m}^2\ \mathrm{s}^{-2}$ and so $F/r \cong 0.08\ \mathrm{m\ s}^{-1}$. With historical estimates of the alongshore transport ($Q \cong -4.0 \times 10^5\ \mathrm{m}^3\ \mathrm{s}^{-1}$), the ratio of boundary- to wind-forced flow at Halifax is approximately,

$$K = \frac{fQ}{2Fy} \cong 1.4.$$

According to Fig. 2b, this means that the current maximum for the combined flow lies closer to $x = 2^{1/2}L_x \cong 45$ km ($\xi = 1$), and that a current reversal is found near the S1

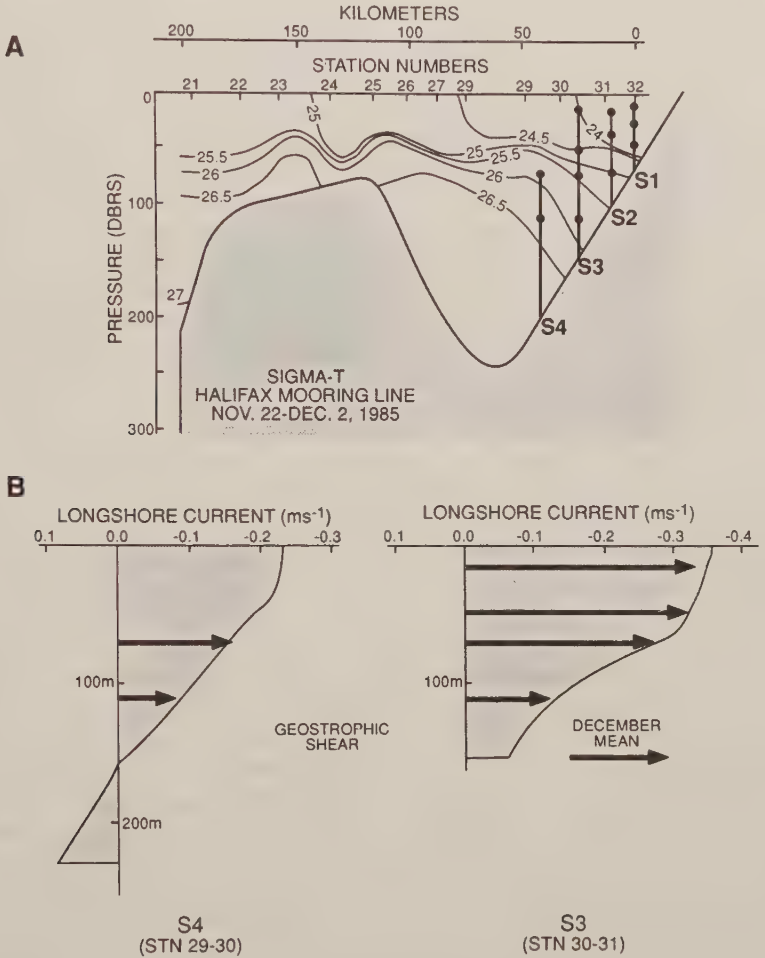


Fig. 7. (A) Cross-shelf density field on the Halifax Section in early December 1985. (B) Geostrophic velocity profiles centred on CASP moorings S4 (Stations 29–30) and S3 (Stations 30–31). Solid arrows represent December mean, measured alongshore currents.

mooring, 20 km from shore, as observed. Furthermore, on the Liscomb line, the value of K is closer to 2.0 ($-y \cong 250$ km) so that the current reversal would lie inshore from the S9 mooring on the 60 m isobath. However, though the structure of the model current field is reasonable, the peak magnitude of the longshore current ($\cong 0.04$ m s^{-1}) is much smaller than observed. Reducing the bottom friction coefficient would improve that comparison, but also shift the axis of the model current further offshore. Considering the neglect of stratification and other barotropic forcing mechanisms (e.g. topographic drag asymmetries; HAIDVOGEL and BRINK, 1986), the agreement between this simple model and the CASP observations must be considered qualitative at best.

In addition, the baroclinic structure of the flow is important. The cross-shelf structure of the density field off Halifax in early December, 1985 (Fig. 7), shows a strong pycnocline at

50–100 m with steeply sloping isopycnals in the nearshore region. The geostrophic shear profiles are remarkably consistent with the measured shear determined from the December mean currents at CASP sites S3 and S4. When fit to the 70 m measured velocities, the geostrophic calculations lead to: (1) depth-averaged currents of 0.27 and 0.12 m s^{-1} at S3 and S4; and (2) significant bottom currents (order 0.10 m s^{-1}) out to the 150 m isobath which have been neglected in the historical transport estimates (Drinkwater *et al.*, 1979). This indicates that the net volume transport at this time contains a large barotropic component, of order 1–2 times the baroclinic component. Clearly, measurements of the density field alone are inadequate for determining either the volume transport or the magnitude and direction of the near-bottom currents. On the other hand, the dynamical origin of the barotropic component of the flow is unknown. Considering the evidence for important buoyancy sources in the Labrador Sea and Gulf of St Lawrence, thermohaline mechanisms such as JEBAR are considered leading candidates for driving the mean coastal circulation.

WIND-DRIVEN VARIABILITY

The response of the Atlantic Canadian coastal ocean to transient wind forcing varies with season. The severe winter weather is due primarily to extratropical cyclones which develop along the eastern seaboard of the U.S. and propagate northeastward along the Polar Front. These storms are organized on a broad range of scales from synoptic (2000 km) to the mesoscale (20–200 km). In coastal waters, synoptic-scale atmospheric forcing is associated with subtidal variability (periods of 2–10 days) while mesoscale forcing is often linked to clockwise-rotating inertial currents (periods from 17–22 h, depending on latitude). Furthermore, surface waves generated by storm winds affect the low-frequency circulation in shallow water through their influence on bottom friction.

In summer, lighter southwesterly winds generally prevail that are punctuated by the occasional intense tropical storm (Drinkwater, 1989). The summer water column is highly stratified and southwesterly winds favour coastal upwelling on the Scotian Shelf and shelf regions of like orientation. Petrie *et al.* (1987b) have used satellite images to demonstrate that persistent summer winds produce a band of cold, upwelled water near the coast that subsequently forms eddies (50 km scale) through baroclinic instability of the upwelling front. Petrie (1983) has also observed baroclinic upwelling and the Scotian Shelf break in winter.

The focus of this section is placed on the wintertime response in shallow ($\leq$100 m), well-mixed water because strong currents are developed, especially near bottom. The storm response described here is characteristic of other regions of the eastern Canadian shelf since the same storms tend to track along the coast.

Subtidal variability

As with the mean and seasonal circulations subtidal variability on the continental shelf may be driven by both local wind and boundary forcing. Energy propagates along the shelf in the "forward" direction via CTWs (Gill and Schumann, 1974; Clarke and Brink, 1985) which are damped by friction and often scattered by topographic irregularities. On the Labrador Shelf, Webster and Narayanan (1988) have demonstrated that CTWs generated by flow through Hudson Strait dominate the subtidal current variability in the northern regions (e.g. Sagalek Bank), but are roughly equivalent to the local wind-forced fluctuations further south (at Nain Bank). This change in relative importance of the two forcing components with downstream distance is a consequence of the scattering and frictional decay of the CTW and the growth of the local response with downshelf distance as in the steady case (Fig. 2b). The forcing mechanism at the northern boundary is related to a Helmholtz-like resonance of the Hudson Bay/Hudson Strait system in response to differential barometric pressure fluctuations over Hudson Bay (Wright *et al.*, 1987) and the flow in Hudson Strait due to along-strait wind stress (Webster and Narayanan, 1988). Results of a linear, barotropic model similar to (1)–(6) show reasonable agreement with observed currents. Discrepancies between the model and observations are attributed to: (1) topographic irregularities; and (2) effects of stratification.

On the Scotian Shelf, Schwing (1989a) has recently used CASP observations to demonstrate the existence of CTWs in the subsurface pressure (SSP) field. Employing multiple regression analysis in the frequency domain he was able to separate the local (L) from the nonlocal (NL) boundary forced response by using the SSP signal very near to the backward boundary ($\mathrm{SSP}^{\mathrm{NL}}$ at Louisbourg, Nova Scotia; see inset, Fig. 6) as a proxy variable for the incident CTW energy. The character of the subtidal SSP response was found to be largely independent of frequency and so could be represented by the results from a single frequency band centred at 0.125 cpd (Fig. 8). The pattern of response to local alongshore wind stress (τ^y) is similar to that of the arrested topographic wave model (12a), suitably modified to include time dependence (Fig. 8, solid curve). Thus the amplitude of the SSP response at the coast increases with alongshore distance to the west (forward direction) as the response diffuses outward across the shelf. On the other hand, the amplitude of the nonlocal SSP response decreases to the west on a decay scale of order 900 km, while the phase propagates westward as expected. Estimated phase speeds at the coast are consistent with those of frictional CTW theory for idealized Scotian Shelf topography.

The regression model containing both components of local (τ^x, τ^y) and remote ($\mathrm{SSP}^{\mathrm{NL}}$) forcing accounts for over 90% of the total SSP variance in the synoptic band at Sambro (near Halifax) (Fig. 9). The relative contributions of alongshore stress and boundary forcings are roughly equal, while the effects of cross-shore stress (τ^x) are much weaker. The importance of alongshore stress relative to boundary forcing increases to the west, in accord with the steady solution (Fig. 2b).

Unlike the pressure variability, CASP current fluctuations were much less coherent with each other or with the forcing variables, particularly local wind stress (Schwing, 1989b). In spite of some substantial contributions from remote forcing at low frequencies (periods >5 days), the amount of alongshore current variance accounted for in the multiple regression analysis ranged between 50 and 80% with the highest values found inshore. Nevertheless, the significant velocity responses at individual moorings were relatively independent of depth; the flow appears to be barotropic. Furthermore, some integral measure of consistency between SSP and alongshore current was found in the fact that the cross-shelf pressure gradients estimated from: (1) the cross-shelf difference in SSP response; and (2) the geostrophic-equivalent pressure difference derived from the cross-sectional average current response, were comparable for both the locally and remotely forced components.

The discrepancy between the spatial coherence scales of SSP and current has also been noted in the Gulf of Maine by Vermersch *et al.* (1979), who speculated that highly

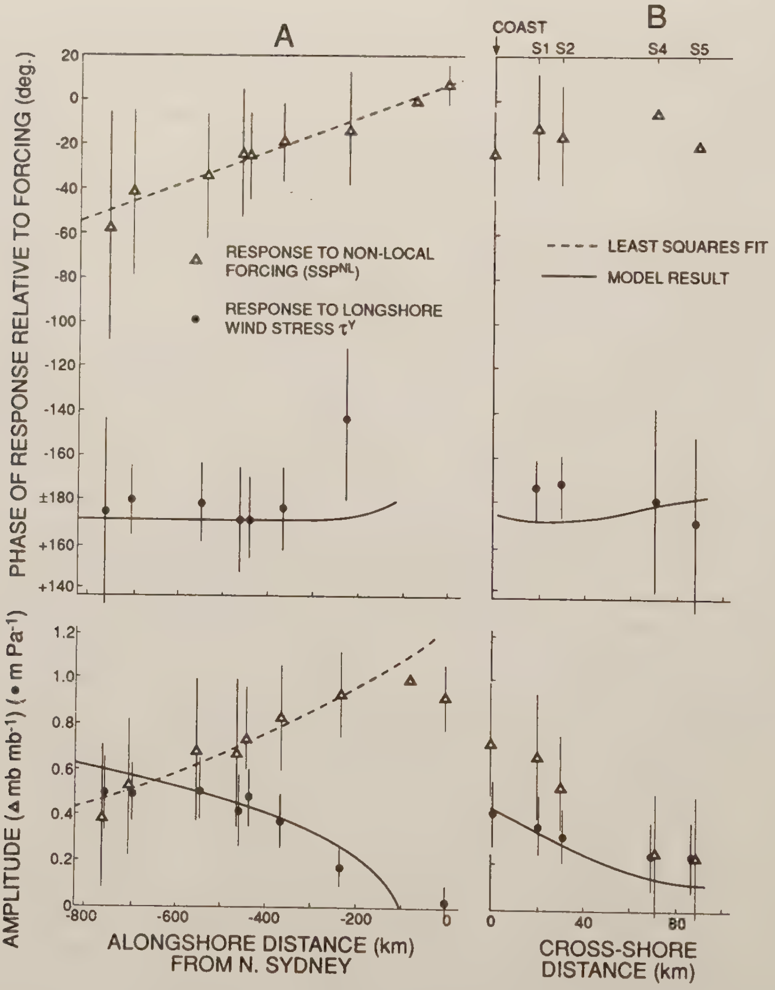


Fig. 8. Phase and amplitude of the 0.125 cpd subsurface pressure (SSP) response to Sable Island alongshelf wind stress, τ^y, and to Louisbourg SSP as a function of (A) alongshelf and (B) cross-shelf distances. Error bars are the 95% confidence limits. Solid curves represent locally forced response of a simple time-dependent model (SCHWING, 1989a) and dashed lines are fits to the nonlocal response.

irregular topography was responsible for generating mesoscale eddies in the current field. SCHWING (1989b) has used a series of simple models with idealized topographic features to demonstrate that vortex stretching, topographic steering and scattering of CTW energy, combined with strong friction, were all important mechanisms affecting the spatial variability of current more so than pressure. For quantitative comparison, he then developed a linearized barotropic model with harmonic time-dependence and realistic Scotian Shelf bathymetry (Fig. 10a). At a frequency of 0.125 cpd, the numerical results for the depth-integrated transport resulting from local (Fig. 10b) and boundary (Fig. 10c)

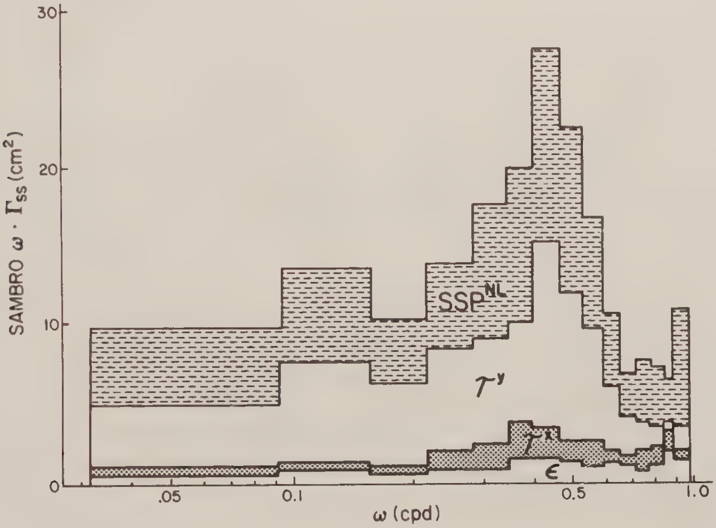
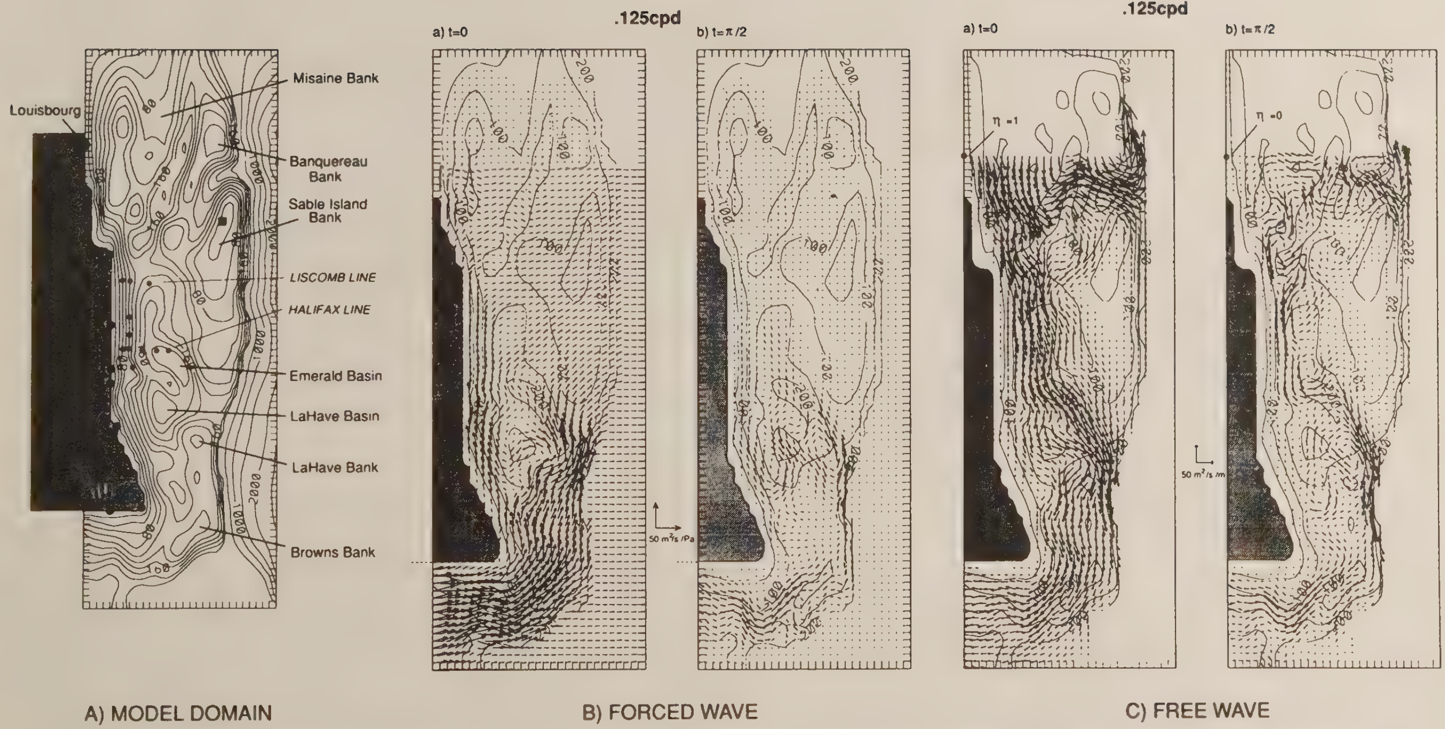


Fig. 9. Distribution of variance in Sambro SSP due to Sable Island wind stress components (τ^x, τ^y) and nonlocal forcing (SSP^{NL}). Region labelled ε represents residual error (<10%).

forcing show a rich complexity of small-scale circulations, superimposed on a background flow with many of the gross features of the idealized models (9) and (12). The alongshore stress (τ^y) applied uniformly over the domain west of Louisbourg, is maximum to the east at $\omega t = 0$ and reversing at $\omega t = \pi/2$. The response generally grows in the forward direction, with a maximum near the coast, but also shows evidence of topographic steering. As the stress reverses, closed circulation cells with scales of 50–100 km are clearly seen in association with topographic features.

The boundary forcing in Fig. 10c is in the form of a mode-1 CTW incident on the cross-shelf (backward) boundary, 140 km east of Louisbourg. The response is normalized to Louisbourg sea level, with unit (zero) amplitude at $\omega t = 0$ ($\pi/2$). For this case, the maximum transports are offshore as the flow is clearly guided away from the shallow regions. Some wave energy is deflected backward or off the shelf and the net transport decreases in the forward direction due to both scattering and frictional dissipation. Again as the flow reverses, there is evidence for small-scale residual features trapped to the topography. Another interesting aspect of the numerical model is that the solutions west of Louisbourg for higher-mode (e.g. mode-2) incident waves are very similar to that for the mode-1 incident wave, both in structure and phase speed. It appears that the higher modes are effectively scattered and dissipated by the rugged shelf bathymetry on a scale smaller than the shelf width, so that only mode-1 survives over the forward portion of the shelf. Thus the boundary-forced response is largely independent of the incident wave form.

At higher frequencies, the same qualitative picture emerges, but the flow is less influenced by topography. Detailed comparisons of model results with CASP alongshore current response (Schwing, 1989b) show approximate agreement in amplitude and phase, especially in the nearshore region and for the remotely-forced component of flow. As


Louisbourg
Misaine Bank
Banquereau Bank
Sable Island Bank
LISCOMB LINE
HALIFAX LINE
Emerald Basin
LaHave Basin
LaHave Bank
Browns Bank
.125cpd
a) t=0
b) t=π/2
50 m²/s /Pa
.125cpd
a) t=0
b) t=π/2
η =1
η =0
50 m²/s /m

A) MODEL DOMAIN B) FORCED WAVE C) FREE WAVE

Fig. 10. Scotian Shelf model transport response to local (B) wind stress and nonlocal (C) boundary-forcings at 0.125 cpd. Wind stress is applied uniformly in the region west (forward) of Louisbourg; remote forcing is in the form of a mode-1 CTW at Louisbourg. The model domain is shown in (A) (from SCHWING, 1989b).

found for the Labrador Shelf, discrepancies in the offshore zone may be caused by baroclinic effects associated with the relatively weak wintertime stratification.

Inertial response

In the deep ocean, the large-scale response to an isolated storm consists of a forced component moving with the storm and a spreading, three-dimensional wake of inertial-gravity waves (PRICE, 1981, 1983). When the storm moves over the stratified waters of the continental shelf, however, the inertial wave field is forced to accommodate: (1) a shallow water column, where the thickness of the deep layer may be the same order as the mixed layer depth; (2) coastal boundaries, which inhibit inertial motions; and (3) frictional dissipation. The character of the inertial response on the shelf is strongly controlled by the relative magnitudes of the storm speed, U, and the characteristic speeds of the barotropic, c_o, and first baroclinic, c_1, modes of the system (KUNDU and THOMSON, 1985). DE YOUNG and TANG (1989) have demonstrated that on the outer regions of the Grand Banks of Newfoundland, isolated, intense autumn storms, for which $c_o \gg U \gg c_1$, generate purely baroclinic inertial waves which may be simulated by an inviscid, one-dimensional, two-layer model driven by observed winds. The responses in the upper and lower layers are 180° out of phase and the inertial transport (current × thickness) is the same in both layers. However, when the scales of the forcing wind field are less well-defined, the model assumptions are violated and the comparison is degraded.

When inertial waves encounter the coast, the condition of no normal flow through the solid boundary causes scattering into other baroclinic modes such that this condition is satisfied (KUNDU, 1986). During CASP, a succession of winter storms over the Scotian Shelf drove a highly intermittent inertial current response, indicated by complex demodulation of the current velocity components at inertial frequencies (Fig. 11c,d; SMITH, 1989a). Peak amplitudes of 0.20 m s^{-1} were reached in the surface layer on the 150 m isobath [S3 (16 m), S11 (11 m); Fig. 11c] during a particularly intense storm (IOP14) on 7 March 1986. On the same isobath, deep inertial currents [S3 (110 m); Fig. 11d] were nearly as strong, but "coastal inhibition" of inertial wave energy was also evident by comparing the surface layer responses on the 60 m isobath [S1 (12 m)] with those further offshore.

To investigate the structure of the inertial response to IOP14, CASP current records were band-pass filtered at the inertial frequency and complex correlated (KUNDU, 1986) with the record from the near-surface instrument at S3 (16 m) over a 3-day period encompassing the storm event. [The magnitude of the complex correlation represents the weighted-average correlation of two vector time series, while the phase gives the average counterclockwise angle (looking downward) of the vector of interest with respect to the reference vector.] The phase on the Halifax mooring line exhibits rapid clockwise turning with depth through the pycnocline (50–70 m) indicating upward phase and downward energy propagation (Fig. 12a). Deep water currents are coherent but out of phase with the surface. However nearshore, the sharp decline of the correlation signals the inhibition of inertial wave energy.

A plan view of the surface-layer average correlation (Fig. 12b) indicates roughly onshore propagation of the rapidly decaying inertial wave. [Note however that differences in spacing of phase lines along the eastern (Liscomb) and western (Halifax) mooring lines suggest that two essentially independent estimates of phase speed exist.] An examination of the synoptic fields of the IOP14 storm (Fig. 13a) shows that peak winds over the Scotian

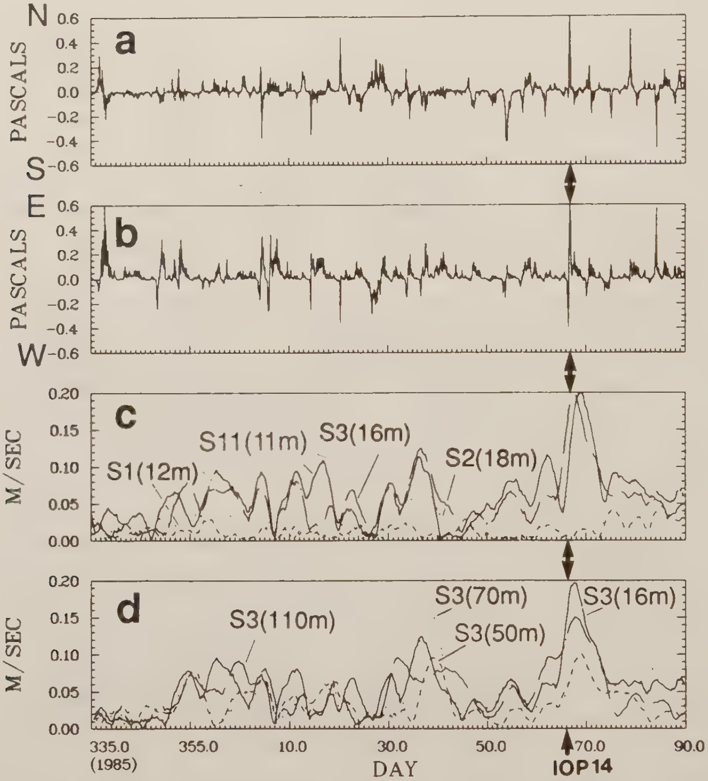


Fig. 11. Time series of Shearwater (see Fig. 6) wind stress and the amplitude of the inertial complex demodulate of the cross-shelf current component. (A) Northward wind stress; (B) eastward wind stress; (C) inertial current amplitude in the surface layer; (D) inertial current through the water column at S3. Solid arrows mark the IOP14 storm (from Smith, 1989a).

Shelf near 1200 GMT on 7 March rotated sharply from easterly to southwesterly in association with a narrow mesoscale warm front within the storm. The mesonet estimate of the velocity of the front, $U \cong 10$ m s^{-1} to the north, is consistent with at least one estimate (8.1 ± 0.9 m s^{-1} on the Liscomb line) of the onshore propagation speed of the inertial currents (the other appears to be contaminated by proximity of the Halifax line to the storm centre; Smith, 1989a). Furthermore, the temperature and density records reveal a baroclinic wave propagating *offshore* at $c_1 \cong 1.8$ m s^{-1} as a result of the coastal adjustment process. These features are qualitatively consistent with numerical model results of Kundu (1986) for the response to a moving front which crosses the coast.

These analyses suggest that inertial currents near the bottom will be most important in shallow, stratified waters away from the coast (i.e. over the outer banks of the shelf). Although some details of the generating mechanism(s) remain obscure, it is clear that intense winter storms play an important role. Because of its significance to sediment transport at the seabed, it is worthwhile to examine some effects of bottom friction associated with storms.

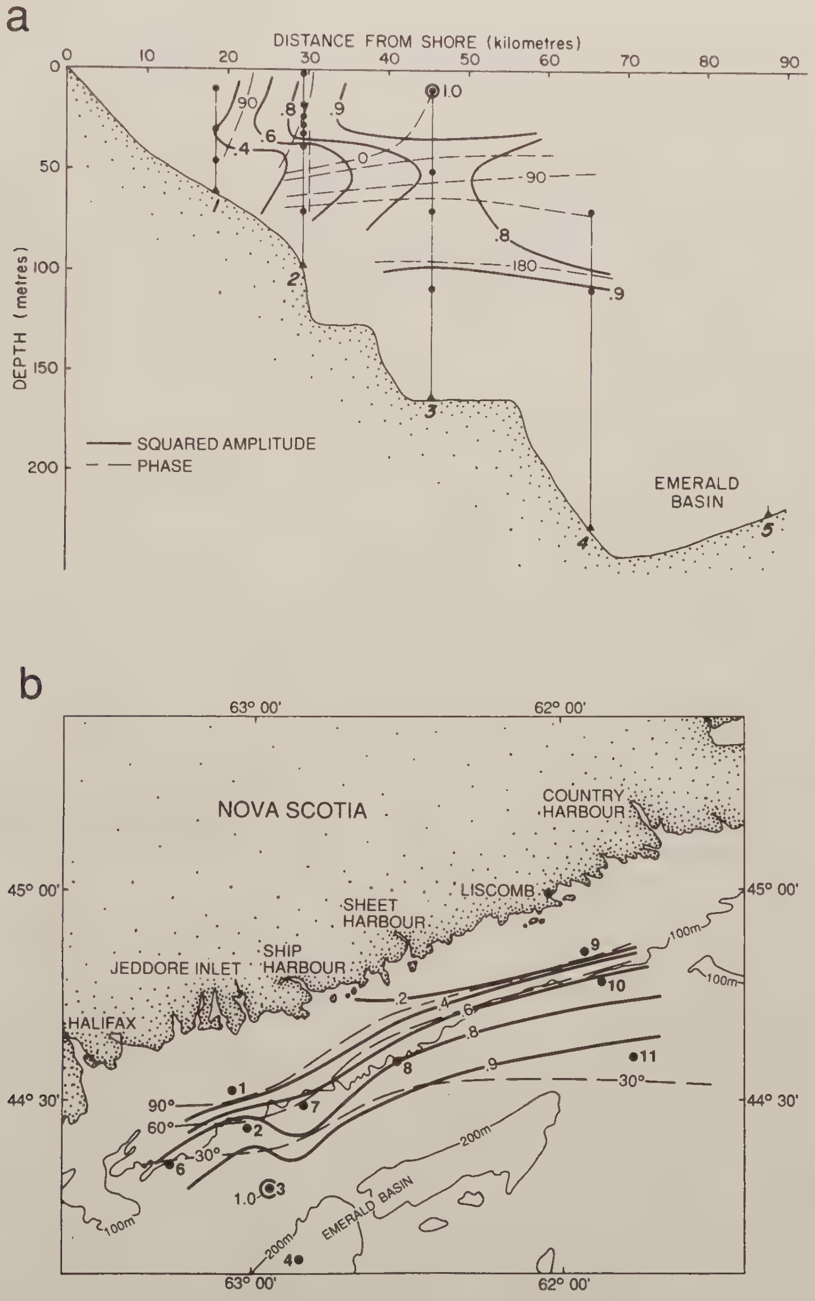


Fig. 12. Contour plot of the magnitude and phase of the squared complex correlation of currents measured during CASP IOP14. (A) Vertical section along the Halifax mooring line; and (B) plan view of the average values in the surface mixed layer (depth <40 m) (from Smith, 1989a).

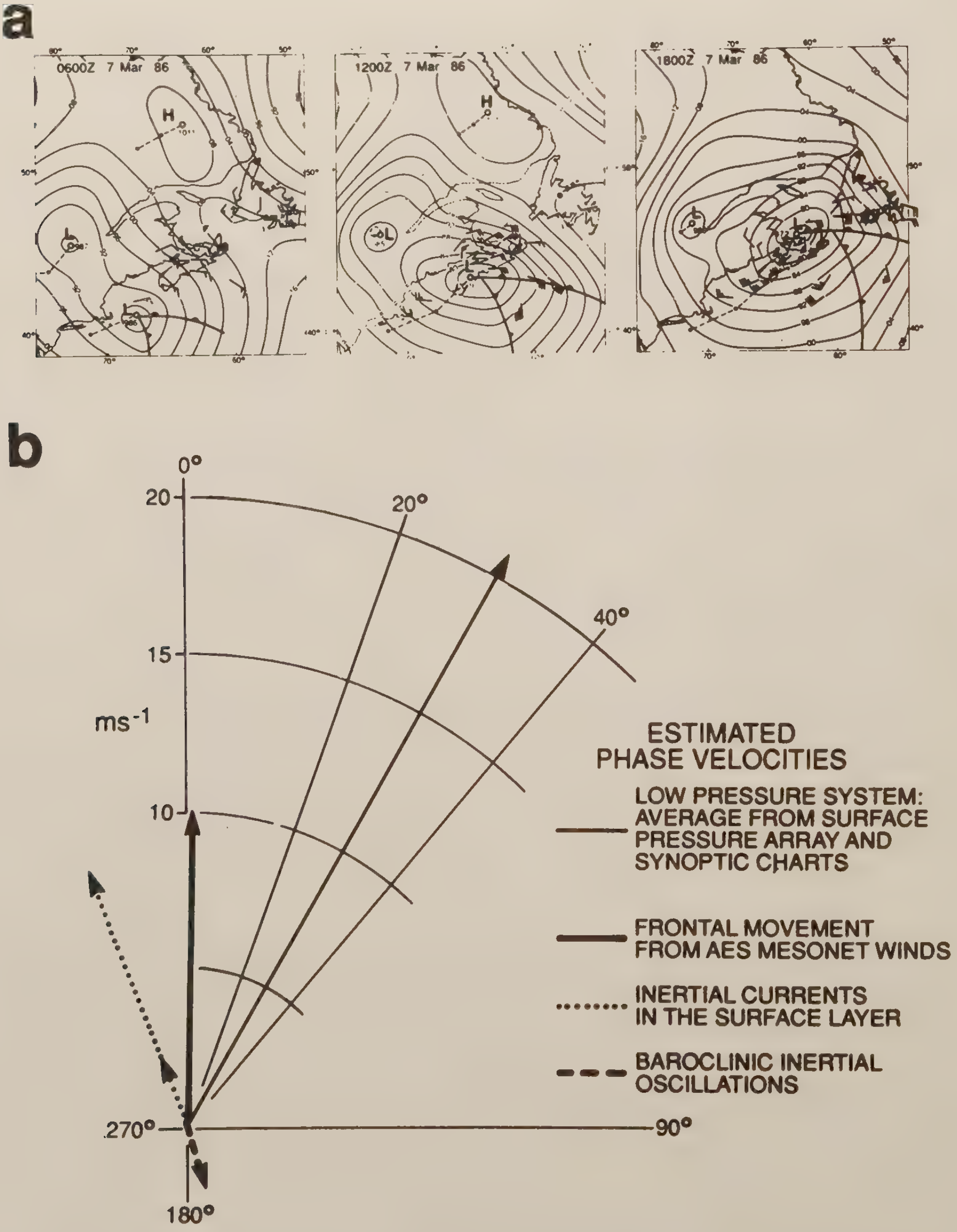


Fig. 13. (A) Synoptic weather charts showing movement of the CASP IOP14 storm across the region during 0600–1800 GMT, 7 March 1986. (B) Estimated phase velocities during CASP IOP14, including motion of the low pressure centre from surface pressure measurements, frontal velocity from mesonet winds, two estimates of onshore propagation of inertial oscillations in the surface layer, and an estimate of the baroclinic phase velocity on the Liscomb mooring line (from Smith, 1989a).

Surface waves and bottom friction

Detailed mapping of the seabed in the nearshore region of the CASP mooring array reveals a wide variety of bottom types (sand, gravel, cobble-boulder lags, bedrock; PIPER, this issue) which lead to substantial variation in bottom roughness [10^{-4} m $< k_s < 1$ m (grain size); $10^{-2} < k_b < 10$ m (bedform); FORBES and DRAPEAU, 1989; FORBES *et al.*, this issue] and that creates resistance to the fluid flow above. Furthermore, during storms the bottom stresses are enhanced by the presence of surface waves which increase the apparent roughness of relatively smooth bottoms through interaction with the current within the wave boundary layer (GRANT and MADSEN, 1979). Under these conditions, it is reasonable to question the conclusion that the inhibition of inertial waves is due entirely to (inviscid) scattering of incident energy at the coastal boundary, and to consider the role of frictional dissipation in shallow water.

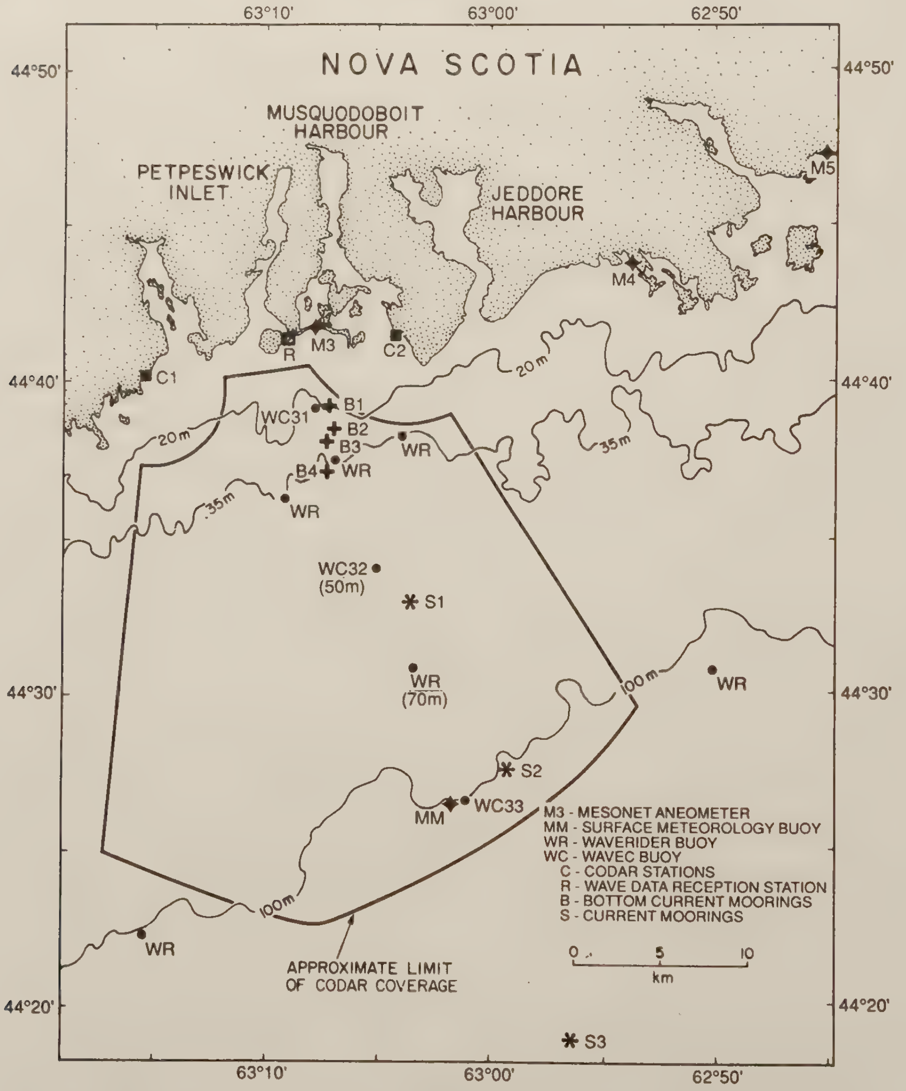
Surface wave measurements were made during CASP with an array of wave riders and directional wave buoys (WAVECs) in the nearshore region off Martinique Beach near Halifax (Fig. 14; DOBSON *et al.*, 1989). In the wake of the IOP14 storm, these instruments recorded significant wave heights from 1.5 to 6.0 m propagating onshore from the east and south, with characteristic periods ranging from 6 to 13 s (Fig. 15). At the same time, nearshore moorings (B1–B4) carrying Aanderaa instruments were measuring currents at 1 m above the bottom in depths ranging from 20 to 37 m as part of a sediment transport study (FORBES and DRAPEAU, 1989). Comparing these currents with those offshore in the surface layer (Fig. 16) clearly shows the shoreward decay of inertial wave energy. Inside the 60 m isobath (S1), all vestiges of the 17-h oscillation disappear and the flow mirrors the wind stress with a small but significant phase lag.

Sample calculations (following MARTEC, 1984) using the GRANT and MADSEN (1979) formulation with observed wave and current data reveal strong temporal and spatial variations of the bottom stress during IOP14, as well as extreme sensitivity to the bottom roughness scales. Near-bottom orbital wave velocities and displacement amplitudes were estimated from the directional wave spectra at the WAVEC sites and currents (u_b, 1 m above the bed) were interpolated from either the measured currents at B1–B4 or estimated deep currents at S1 and S2. The resulting time-averaged bottom shear stress, $|u_{*c}|^2$, is related to the bottom resistance coefficient, r, by

$$r(x, t) = |u_{*c}|^2/|u_b|.$$

Following FORBES and DRAPEAU (1989), the minimum stresses were obtained for a flat, immobile bed of uniform sand ($D = 0.2$ m) with nominal bed roughness of $k_b = 30\,D$. The cross-shelf profiles of $r(x, t)$ show dramatic variations (Fig. 17a). On the 100 m isobath (WC33, 30 km from shore), the resistance coefficient lies between 1 and 2×10^{-4} m s^{-1} until the 13 s waves arrive at 2400 GMT, day 66, that is, roughly 12 h after the storm centre passed over the Scotian Shelf off Halifax (Fig. 13a). At 1200 GMT, those values apply to the entire region, while at 2400 GMT, r increases shoreward by more than a factor of two. The maintenance of significant currents and large, long-period waves over the succeeding 12 h suggests that the 2400 GMT profile remains well into the following day.

When the grain (k_s) and bedform (k_b) roughness scales of the sea floor are increased over the range corresponding (approximately) to rippled sand and gravel beds (FORBES and DRAPEAU, 1989) the estimated resistance coefficients at 2400 GMT are augmented by an order of magnitude. The maximum values of k_s and k_b are attributed to large-scale,


63°10'
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NOVA SCOTIA
MUSQUODOBOIT HARBOUR
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JEDDORE HARBOUR
M5
M4
M3
R
C1
C2
20m
35m
100m
WC31
B1
B2
B3
B4
WR
WC32 (50m)
S1
WR (70m)
S2
MM
WC33
S3
M3 - MESONET ANEOMETER
MM - SURFACE METEOROLOGY BUOY
WR - WAVERIDER BUOY
WC - WAVEC BUOY
C - CODAR STATIONS
R - WAVE DATA RECEPTION STATION
B - BOTTOM CURRENT MOORINGS
S - CURRENT MOORINGS
0 5 10
km
APPROXIMATE LIMIT OF CODAR COVERAGE

Fig. 14. Locations of CASP nearshore surface wave and current measurement arrays. Along the main line, directional wave measurements were obtained from the WAVEC buoys (WC) while currents were measured through the water column (S1–S3) and near the bottom (B1–B4). High-frequency radar (CODAR) was also used to detect surface currents and wave spectra to roughly 30 km from shore.

wave-formed ripples in gravel having wavelengths of $1 < \lambda < 3$ m and ripple heights of $0.2 < \eta < 0.4$ m. Even greater scales might be associated with observed cobble-boulder lags in the region, but their effects are not easily parameterized. For comparison with these estimates, the cross-shelf profile, $r(x)$, used by Chapman (1986) and Chapman *et al.* (1986) for modelling steady barotropic flow is included in Fig. 17a. This form is said to represent a compromise between: (1) the Grant and Madsen model for 1 m, 15 s waves, and a 0.15 m s^{-1} steady current; and (2) empirical estimates of bottom friction on the shelf and slope.

The importance of friction in damping nearshore inertial energy may be estimated by comparing the inertial time scale, $T_I = f^{-1}$, to the frictional spindown time, $T_B = h/r$. For

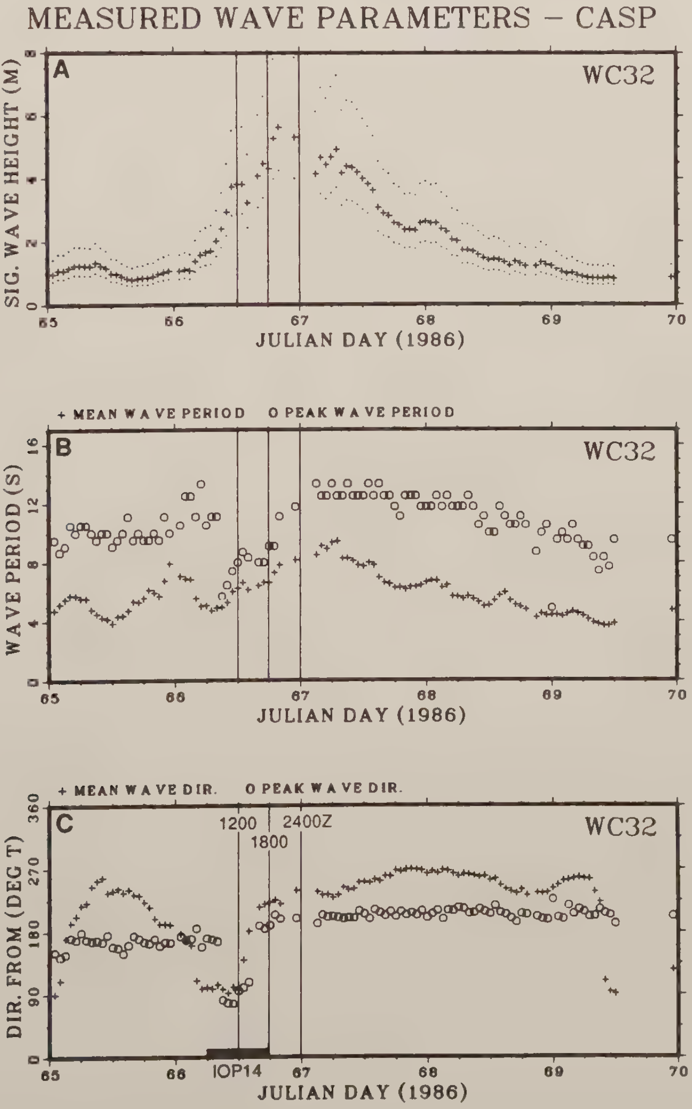

Fig. 15. Measured surface wave parameters during CASP IOP14 at the central WAVEC buoy (WC32). (A) Significant wave height; (B) mean and spectral peak wave period; and (C) mean and spectral peak wave direction. Dotted curves in (A) represent 90% confidence limits on wave height.

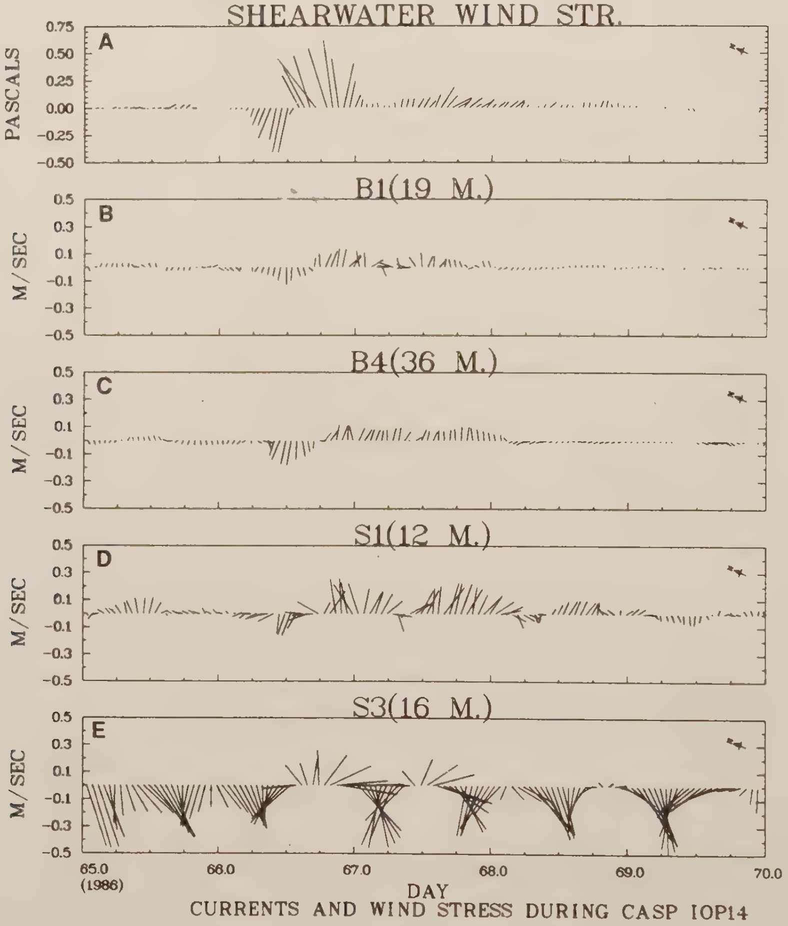

Fig. 16. Shearwater wind stress and cross-shelf distribution of currents during CASP IOP14. Currents at S1 and S3 are from the surface layer, while B4 and B1 were measured at 1 m above the bottom. Longshore direction (68°T) for current and wind is vertically upward on this page.

the flat sandy bed, the minimum value of the ratio, T_B/T_1 (Fig. 17b), exceeds three for the site nearest the shore under the influence of the largest and longest-period waves. This would suggest that significant frictional damping would occur only over several inertial periods, in contrast to the observations which indicate that the inhibition process is immediate and complete. However, for a mobile bed of coarse gravel, the ratio approaches unity in shallow water, so that significant damping might occur on the inertial time scale.

Another way to gauge the importance of friction in shallow water is to consider the dynamics of the wind-driven current. If the cross-shelf current is considered small near the coast, then (2) relates the longshore current to the driving wind. Using wind data from the MINIMET buoy (similar to that in Fig. 16a) during 0600 GMT, day 66 to 0600 GMT, day 67, the longshore stress may be approximated as

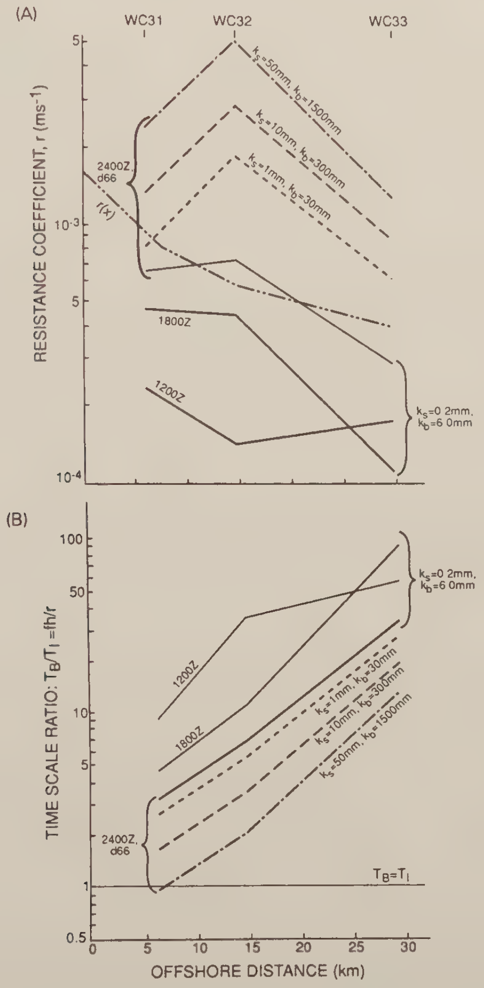

Fig. 17. (A) Cross-shelf distributions (solid curves) of the bottom resistance coefficient, r, with nominal roughness scales ($k_s = 0.2$ mm, $k_b = 6.0$ mm) as a function of time during CASP IOP14. Broken curves represent the sensitivity of the 2400 GMT cross-shelf profile to the observed range of bottom roughness scales. Also shown is the steady parameterization, $r(x)$, of CHAPMAN *et al.* (1986). (B) Cross-shelf distributions of ratio of bottom frictional spindown time, $T_B = h/r$, to inertial time scale, $T_I = f^{-1}$.

$$\tau^y = \tau_o \cos \omega t, \tag{14}$$

where $\omega \cong 2\pi$ per 24 h. With $u = 0$, (2) reduces to

$$v_t + \frac{rv}{h} = \frac{\tau^y}{\rho h} - g\zeta_y \tag{15}$$

where ζ_y is considered a constant. Neglecting transients, the solution for harmonic forcing (14) is

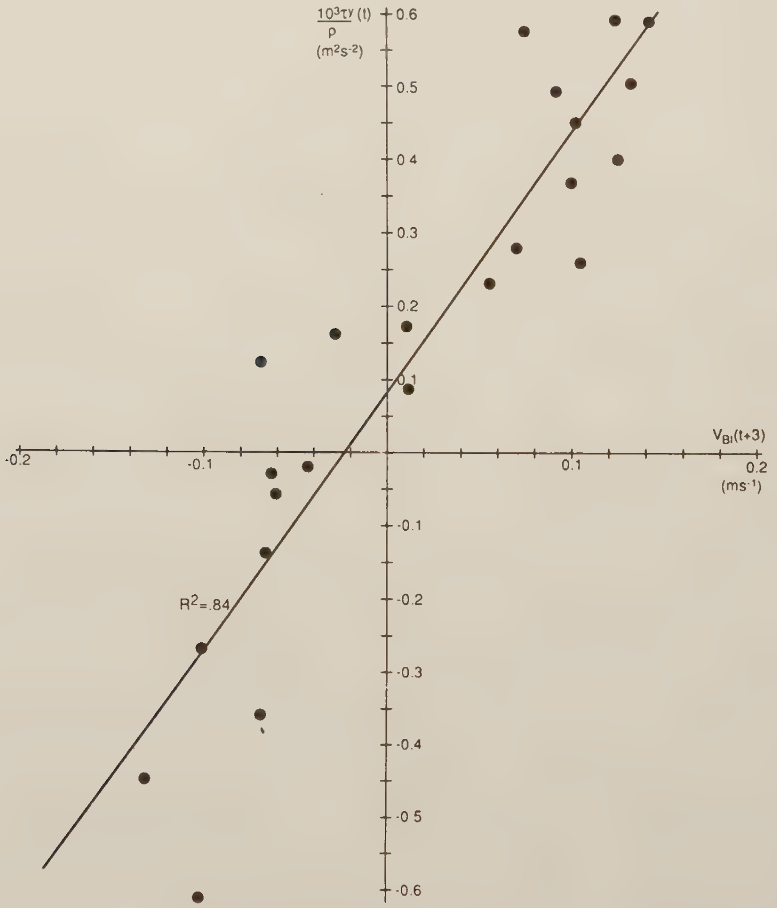

Fig. 18. Scatter plot of hourly kinematic alongshore wind stress at the MINIMET buoy (see Fig. 14) versus alongshelf bottom current at mooring B1, lagged by 3 h. Wind stress records cover the passage of the IOP14 storm (0600 GMT, day 66 to 0600 GMT, day 67). The linear regression of $10^3\tau^y(t)/\rho$ on $v_{B1}(t + 3\text{ h})$ has a regression coefficient of $R^2 = 0.839$.

$$v = \frac{\tau_o}{\rho r}\cos(\omega t - \phi) - \frac{gh}{r}\zeta_y \qquad (16)$$

where $\tan\phi = \omega h/r$. Lagged correlation analysis of the MINIMET hourly alongshore stress component and near-bottom currents on mooring B1 ($h = 20$ m) indicates that the maximum correlation occurs when v_{B1} lags τ^y by 3 h. This implies that $\phi = \pi/4$, $\omega h/r = \tan\phi = 1$, so $r = 1.5 \times 10^{-3}\ \text{m s}^{-1}$. Furthermore, the slope of the linear regression of $10^3\,\tau^y(t)/\rho$ against $v_{B1}(t + 3\text{ h})$ indicates that $r = 3.6 \pm 0.4 \times 10^{-3}\ \text{m s}^{-1}$ (Fig. 18). These two estimates are not inconsistent with those derived at 2400 GMT from the Grant and Madsen theory for waves over a rippled gravel seabed. Thus the flow along the 20 m isobath feels a resistance much greater than that associated with a sandy bottom. It is tempting to conclude therefore that friction plays some significant role in damping inertial waves in shallow water. However, the absence of inertial oscillations at B4 on the 37 m isobath, where the friction is weaker, suggests that the rapid cancellation of the incident waves by scattering is the more likely mechanism.

Finally, according to (16), the intercept a_o, of the regression line in Fig. 18 is related to the alongshore sea level gradient by

$$\zeta_y = \frac{ra_o}{gh} \cong 6\text{–}14 \times 10^{-7}. \tag{17}$$

Estimates of this order have been obtained elsewhere on the East Coast (SCOTT and CSANADY, 1976; SMITH, 1983). In the shallow coastal zone, however, this force is dominated by those associated with surface wind and bottom stresses, as in the steady case (12).

DISCUSSION

The focus of this review has been to describe and interpret certain aspects of the structure and variability of the mean and wind-driven circulations on the continental shelves of eastern Canada. The emphasis has been on barotropic flow and the effects of topography and bottom friction on that flow. For modelling purposes, the inclusion of reasonable friction is required to reproduce the qualitative features of the circulation. Another important idea for understanding shelf circulation is the necessity to consider both the locally and remotely forced components of the circulation. In the barotropic case, these have distinctly different along- and cross-shelf structures, so that each may be dominant in a different region of the shelf. Finally, the prevalence of rugged shelf topography off eastern Canada renders the current field much less coherent than the subsurface pressure or forcing wind fields. This aspect is clearly demonstrated by the Scotian Shelf model (Fig. 10), which reveals small circulation patterns and phase variations in the time-dependent flow field (SCHWING, 1989b).

Regarding the structure of coastal currents, several important physical effects have also been omitted from this discussion. Tidal friction and vertical mixing strongly influence conditions in the Gulf of Maine, for instance. SMITH's (1983b) diagnostic model suggests that the bottom friction coefficient, r, associated with M_2 tidal currents on the 60 m isobath off southwest Nova Scotia may be as large as 2.4×10^{-3} m s^{-1}, consistent with the maximum values from the nearshore zone during CASP (Fig. 17a), and that horizontal density gradients maintained by gradients in tidal mixing (LODER and GREENBERG, 1986) are dynamically significant. Furthermore, the three-dimensional numerical model of TEE *et al.* (1987) shows that strong tidal friction affects the vertical shear and orientation of tidal and residual currents throughout the water column in parts of the eastern Gulf of Maine. However, vertical stratification associated with seasonal buoyancy input to the region acts to reduce the vertical eddy viscosity to 20% of its value in well-mixed water.

On smaller scales, the flow of the barotropic tide generates trains of high-frequency, large-amplitude internal waves in stratified waters at sharp changes in topography, such as the shelf break or the edges of banks and ridges (HAURY *et al.*, 1979; SANDSTROM and ELLIOTT, 1984). Strong bottom current pulses associated with these waves are often sufficient to resuspend sediment in the vicinity of the generation site (BUTMAN, 1987; BOCZAR-KARAKIEWICZ *et al.*, this issue).

Other aspects of stratification, such as the JEBAR mechanism (Shaw and Csanady, 1983; Huthnance, 1984) for inducing mean currents through interaction of density and topographic gradients, baroclinic modifications of CTWs, and eddy generation through baroclinic instability, have also been neglected. Unstable baroclinic eddies associated with the Labrador Current may exert a direct influence on the shelf circulation, as suggested by satellite observations (LeBlond, 1982) and eddy statistics derived from iceberg drift (Garrett *et al.*, 1985). In addition, the horizontal diffusion associated with an unstable eddy field may act to regulate the JEBAR forcing mechanism by smoothing the density field and reducing the baroclinic currents that drive the instability (Huthnance, 1984).

With regard to CTWs, Webster and Narayanan (1988) have attributed significant vertical phase differences in the low-frequency current response on the Labrador Shelf to the combination of local topographic and stratification effects as measured by the stratification parameter: $S = (Ns/f)^2$, where s is the local bottom slope and N is the Brunt–Vaisala frequency. Schwing (1989b) also suggested that baroclinic effects might be responsible for discrepancies between wind-forced responses of the Scotian Shelf model and the CASP observations.

Finally, although the direct dynamical influence of the offshore, basin-scale pressure field on the barotropic shelf circulation has been largely discounted, Chapman *et al.* (1986) have demonstrated that the presence of a large-scale oceanic gyre just off the shelf counteracts the offshore migration of streamlines caused by bottom friction. The result is a "dynamical barrier" which confines the coastal alongshore transport to the shelf and allows properties of the source waters to be detected far downstream. A similar process might also operate in the northern region of the Labrador Shelf where the alongshore pressure gradient associated with the circulation in the Labrador Sea would act to constrain the Labrador Current to the shelf edge as observed. Further south, where the North Atlantic Current starts to impinge on the shelf region, the alongshore pressure gradient would be weakened or reversed so that the barrier to offshore migration would be reduced. This might explain the consistent loss of surface drifters from the southern end of the Labrador Shelf (Petrie and Anderson, 1983).

CONCLUSIONS

The main conclusions of this study are summarized as follows.

(a) The mean and seasonal circulations on the continental shelf of eastern Canada appear to be related to buoyancy fluxes associated with runoff and ice-melt in northern waters. The barotropic and baroclinic components of flow are of the same order on both the Labrador Shelf and the Scotian Shelf, but the dynamics of the mechanisms which give rise to them are presently unknown. Seasonal variations in the circulation and water properties (especially salinity and oxygen isotope ratio) are useful for detecting buoyancy sources. The absence of a strong ^{18}O signature of the St Lawrence freshwater runoff in the Gulf of St Lawrence and on the Scotian Shelf is puzzling and should be explored.

(b) The structure of the barotropic mean circulation and wind-driven subtidal variability are influenced by bottom friction which resists both locally and remotely forced components of the flow. These two components are distinguished by their distinctly different horizontal structures: the response to local wind is maximum near the coast and increases alongshore in the forward direction; remotely forced CTWs have maximum transports in the deeper regions of the shelf and decay in the forward (propagation) direction. Current fields associated with both components are strongly influenced by irregular shelf topography through vortex stretching and topographic steering, while high-mode CTWs are scattered and dissipated efficiently.

(c) Inertial waves generated by intense winter storms in stratified shelf waters are strongly baroclinic over the open shelf and inhibited near the coast (within the 60 m isobath). Frictional dissipation, enhanced by surface waves and extreme bottom roughness, is capable of damping the incident energy on inertial time scales in the shallow coastal zone ($\leq$20 m), but the dominant mechanism for coastal inhibition of inertial waves appears to be scattering at the boundary. This process produces energetic inertial currents in the deep water below the winter pycnocline.

(d) The observed wind-driven response in the coastal zone during CASP lags the surface stress forcing by 3 h and is consistent with resistance coefficients, r, of order $1\text{–}4 \times 10^{-3}$ m s^{-1}. These values correspond to the large bottom roughness scales estimated for the seabed in the nearshore region of the Scotian Shelf.

Future studies of coastal circulation should be directed toward increased understanding of the baroclinic components of the mean and low-frequency circulation. The JEBAR mechanism for generating barotropic transport from the interaction of density gradients with steep topography is a prime candidate for modelling studies and comparison with existing observations. Determining the barotropic component of flow is of particular importance for sediment transport since it dictates the magnitude of the mean bottom current. Modelling the baroclinic modifications to frictional CTWs would also increase our understanding of the vertical structure subtidal variability and its implications for near bottom currents. Careful parameterization of friction in the presence of surface waves should be considered for these models.

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REFERENCES

AMOS C. L. and J. T. JUDGE (this issue) Sediment transport on the eastern Canadian continental shelf. *Continental Shelf Research*, **11**, 1037–1068.

ANDERSON C. and P. C. SMITH (1989) Oceanographic observations on the Scotian Shelf during CASP. *Atmosphere–Ocean*, **27**, 130–156.

BEARDSLEY R. C. and C. D. WINANT (1979) On the mean circulation in the Mid-Atlantic Bight. *Journal of Physical Oceanography*, **9**, 612–619.

BOCZAR-KARAKIEWICZ B., J. L. BONA and B. PELCHAT (this issue) Interaction of internal waves with the seabed of the eastern Canadian continental shelf. *Continental Shelf Research*, **11**, 1181–1197.

BRINK K. H. (1986) Topographic drag due to barotropic flow over the continental shelf and slope. *Journal of Physical Oceanography*, **16**, 2150–2158.

BRINK K. H. and J. S. ALLEN (1978) On the effect of bottom friction on barotropic motion over the continental shelf. *Journal of Physical Oceanography*, **8**, 919–922.

BUTMAN B. (1987) Physical processes causing sediment movement. In: *Georges Bank*, Ch. 13, R. BACKUS, editor, MIT Press, Cambridge, MA, pp. 147–162.

Chapman D. C. (1986) A simple model of the formation and maintenance of the shelf/slope front in the Middle Atlantic Bight. *Journal of Physical Oceanography*, **16**, 1273–1279.

Chapman D. C. and K. H. Brink (1987) Shelf and slope circulation induced by fluctuating offshore forcing. *Journal of Geophysical Research*, **92**, 11741–11759.

Chapman D. C. and R. C. Beardsley (1989) On the origin of shelf water in the Middle Atlantic Bight. *Journal of Physical Oceanography*, **19**, 384–391.

Chapman D. C., J. A. Barth, R. C. Beardsley and R. G. Fairbanks (1986) On the continuity of mean flow between the Scotian Shelf and the Middle Atlantic Bight. *Journal of Physical Oceanography*, **16**, 758–772.

Clarke A. J. and K. H. Brink (1985) The response of stratified, frictional flow of shelf and slope waters to fluctuating large-scale, low-frequency wind forcing. *Journal of Physical Oceanography*, **15**, 439–453.

Csanady G. T. (1976) Mean circulation in shallow seas. *Journal of Geophysical Research*, **81**, 5389–5399.

Csanady G. T. (1978) The arrested topographic wave. *Journal of Physical Oceanography*, **8**, 47–62.

Csanady G. T. (1981) Shelf circulation cells. *Philosophical Transactions of the Royal Society of London*, **A302**, 511–530.

Csanady G. T. (1982) *Circulation in the coastal ocean*, Reidel, Dordrecht, Holland, 279 pp.

Csanady G. T. and P. T. Shaw (1983) The "insulating" effect of a steep continental slope. *Journal of Geophysical Research*, **88**, 7519–7524.

de Young, B. and C. L. Tang (1989) Storm forced baroclinic near-inertial currents on the Grand Bank. *Journal of Physical Oceanography*, **20**, 1725–1741.

Dobson F., W. Perrie and B. Toulany (1989) On the deep-water fetch laws for wind-generated surface gravity waves. *Atmosphere–Ocean*, **27**, 210–236.

Drinkwater K. F. (1989) The response of an open embayment to near-hurricane force winds. *Continental Shelf Research*, **9**, 823–839.

Drinkwater K. F., B. Petrie and W. H. Sutcliffe Jr (1979) Seasonal geostrophic volume transports along the Scotian Shelf. *Estuarine and Coastal Marine Sciences*, **2**, 17–27.

Forbes D. L. and G. Drapeau (1989) Near-bottom currents and sediment transport on the inner Scotian Shelf: Sea-floor response to winter storms during CASP. *Atmosphere–Ocean*, **27**, 258–278.

Forbes D. L., R. Boyd and J. Shaw (this issue) Late Quaternary sedimentation and sea level changes on the inner Scotian shelf. *Continental Shelf Research*, **11**, 1155–1179.

Gatien M. G. (1976) A study in the slope water region south of Halifax. *Journal of the Fisheries Research Board of Canada*, **33**, 2213–2217.

Gill A. E. and E. H. Schumann (1974) The generation of long shelf waves by the wind. *Journal of Physical Oceanography*, **4**, 83–90.

Grant W. D. and O. S. Madsen (1979) Combined wave and current interaction with a rough bottom. *Journal of Geophysical Research*, **84**, 1797–1808.

Greenberg D. A. (1983) Modelling the barotropic circulation in the Bay of Fundy and Gulf of Maine. *Journal of Physical Oceanography*, **13**, 888–906.

Greenberg D. A. and C. L. Amos (1983) Suspended sediment transport and deposition modeling in the Bay of Fundy, Nova Scotia—a region of potential tidal power development. *Canadian Journal of Fisheries and Aquatic Sciences*, **40**, (Suppl. 1), 20–34.

Greenberg D. A. and B. D. Petrie (1988) The mean barotropic circulation on the Newfoundland Shelf and Slope. *Journal of Geophysical Research*, **93**, 15541–15550.

Garrett C., J. F. Middleton, M. Hazen and F. Majaess (1985) Tidal currents and eddy statistics from iceberg trajectories off Labrador. *Science*, **227**, 1333–1335.

Griffiths D. K., R. D. Pingree and M. Sinclair (1981) Summer tidal fronts in the near-arctic regions of Foxe Basin and Hudson Bay. *Deep-Sea Research*, **28**, 865–873.

Haidvogel D. B. and K. H. Brink (1986) Mean currents driven by topographic drag over the continental shelf and slope. *Journal of Physical Oceanography*, **16**, 2159–2171.

Haury L. R., M. G. Briscoe and M. H. Orr (1979) Tidally-generated internal wave packets in Massachusetts Bay. *Nature*, **278**, 312–317.

Houghton R. W., P. C. Smith and R. O. Fournier (1978) A simple model for cross-shelf mixing on the Scotian Shelf. *Journal of the Fisheries Research Board of Canada*, **35**, 414–421.

Huthnance J. M. (1984) Slope currents and "JEBAR". *Journal of Physical Oceanography*, **14**, 795–810.

Kelly K. A. and D. C. Chapman (1988) The response of stratified shelf and slope waters to steady offshore forcing. *Journal of Physical Oceanography*, **18**, 906–925.

KUNDU P. (1986) A two-dimensional model of inertial oscillations generated by a propagating wind. *Journal of Physical Oceanography*, **16**, 1399–1411.

KUNDU P. and R. E. THOMSON (1985) Inertial oscillations due to a moving front. *Journal of Physical Oceanography*, **15**, 1076–1084.

LEBLOND P. H. (1982) Satellite observations of Labrador Current undulations. *Atmosphere–Ocean*, **20**, 129–142.

LODER J. W. (1980) Topographic rectification of tidal currents on the sides of Georges Bank. *Journal of Physical Oceanography*, **10**, 1399–1416.

LODER J. W. and D. A. GREENBERG (1986) Predicted positions of tidal fronts in the Gulf of Maine region. *Continental Shelf Research*, **6**, 397–414.

LOUIS J. P. and P. C. SMITH (1982) The development of the barotropic radiation field of an eddy over a slope. *Journal of Physical Oceanography*, **12**, 56–73.

LOUIS J. P., B. D. PETRIE and P. C. SMITH (1982) Observations of topographic Rossby waves on the continental margin off Nova Scotia. *Journal of Physical Oceanography*, **12**, 47–55.

MARTEC LIMITED (1984) SED1D: A sediment transport model for the continental shelf. Unpublished report to the Geological Survey of Canada, DSS Contract IOSC.23420-3-m753, 63 pp.

MYERS R. A., S. A. AKENHEAD and K. DRINKWATER (1989) The influence of ice-melt and Hudson Bay runoff on the salinity of the Newfoundland Shelf. *Atmosphere–Ocean*, in press.

PETRIE B. (1983) Current response at the shelf break to transient wind forcing. *Journal of Geophysical Research*, **88**, 9567–9578.

PETRIE B. and C. ANDERSON (1983) Circulation on the Newfoundland continental shelf. *Atmosphere–Ocean*, **21**, 207–226.

PETRIE, B., K. LANK and S. DE MARGARIE (1987a) Tides on the Newfoundland Grand Banks. *Atmosphere–Ocean*, **25**, 10–21.

PETRIE, B., B. J. TOPLISS and D. G. WRIGHT (1987b) Coastal upwelling and eddy development off Nova Scotia. *Journal of Geophysical Research*, **29**, 12,979–12,991.

PIPER D. J. W. (this issue) Seabed geology of the eastern Canadian continental shelf. *Continental Shelf Research*, **11**, 000–000.

PRICE J. F. (1981) The upper ocean response to a moving hurricane. *Journal of Physical Oceanography*, **11**, 153–175.

PRICE J. F. (1983) Internal wave wake of a moving storm. Part I: Scales, energy budget and observations. *Journal of Physical Oceanography*, **13**, 949–965.

SANDSTROM H. and J. A. ELLIOTT (1984) Internal tide and solitons on the Scotian Shelf: A nutrient pump at work. *Journal of Geophysical Research*, **89**, 6415–6426.

SCHWING F. B. (1989a) Subtidal response of the Scotian Shelf bottom pressure field to meteorological forcing. *Atmosphere–Ocean*, **27**, 157–180.

SCHWING F. B. (1989b) *Subinertial circulation on the Scotian Shelf: observations and models*. PhD thesis, Department of Oceanography, Dalhousie University, Halifax, Nova Scotia, Canada, 206 pp.

SCOTT J. T. and G. T. CSANADY (1976) Nearshore currents off Long Island. *Journal of Geophysical Research*, **81**, 5401–5409.

SHAW P. T. and G. T. CSANADY (1983) Self-advection of density perturbations on a sloping continental shelf. *Journal of Physical Oceanography*, **13**, 769–782.

SMITH P. C. (1978) Low-frequency fluxes of momentum, heat, salt and nutrients at the edge of the Scotian Shelf. *Journal of Geophysical Research*, **83**, 4079–4096.

SMITH P. C. (1983a) Eddies and coastal interactions. In: *Eddies in marine science*, A. R. ROBINSON, editor, Springer-Verlag, Berlin, pp. 446–480.

SMITH P. C. (1983b) The mean and seasonal circulation off southwest Nova Scotia. *Journal of Physical Oceanography*, **13**, 1034–1054.

SMITH P. C. (1989a) Inertial oscillations near the coast of Nova Scotia during CASP. *Atmosphere–Ocean*, **27**, 181–209.

SMITH P. C. (1989b) Seasonal and interannual variability of current, temperature and salinity off southwest Nova Scotia. *Canadian Journal of Fisheries and Aquatic Sciences*, **46** (Suppl. 1), 4–20.

SMITH P. C., B. PETRIE and C. R. MANN (1978) Circulation, variability and dynamics of the Scotian Shelf and Slope. *Journal of the Fisheries Research Board of Canada*, **35**, 1067–1083.

SUTCLIFFE W. H. Jr, R. H. LOUCKS and K. F. DRINKWATER (1976) Coastal circulation and physical oceanography of the Scotian Shelf and Gulf of Maine. *Journal of the Fisheries Research Board of Canada*, **33**, 98–115.

Tee K. T., P. C. Smith and D. Lefaivre (1987) Modelling and observations of the residual current off southwest Nova Scotia. In: *Three-dimensional models of marine and estuarine dynamics*, J. C. J. Nihoul and B. M. Jamart, editors, Elsevier, Amsterdam, pp. 455–470.

Tee K. T., P. C. Smith and D. Lefaivre (1988) Estimation and verification of tidally-induced residual currents. *Journal of Physical Oceanography*, **18**, 1415–1434.

Vermersch J. A., R. C. Beardsley and W. S. Brown (1979) Winter circulation in the western Gulf of Maine: Part 2. Current and pressure observations. *Journal of Physical Oceanography*, **9**, 768–784.

Wang D. P. (1982) Effects of continental slope on the mean shelf circulation. *Journal of Physical Oceanography*, **12**, 1524–1526.

Weaver A. J. and W. W. Hsieh (1987) The influence of buoyancy flux from estuaries on the continental shelf circulation. *Journal of Physical Oceanography*, **17**, 2127–2140.

Webster I. and S. Narayanan (1988) Low-frequency current variability on the Labrador Shelf. *Journal of Geophysical Research*, **93**, 8163–8173.

Wright D. G. (1986) On quasi-steady shelf circulation driven by along-shelf wind stress and open-ocean pressure gradients. *Journal of Physical Oceanography*, **16**, 1712–1714.

Wright D. G. (1989) On the along-shelf evolution of an idealized density front. *Journal of Physical Oceanography*, **19**, 532–541.

Wright D. G. and J. W. Loder (1988) On the influences of nonlinear bottom friction on the topographic rectification of tidal currents. *Geophysical and Astrophysical Fluid Dynamics*, **42**, 227–245.

Wright D. G., D. A. Greenberg, J. W. Loder and P. C. Smith (1986) The steady-state barotropic response of the Gulf of Maine and adjacent regions to surface wind stress. *Journal of Physical Oceanography*, **16**, 947–966.

Wright D. G., D. A. Greenberg and F. G. Majaess (1987) The influence of bays on adjusted sea level over adjacent shelves with application to the Labrador Shelf. *Journal of Geophysical Research*, **92**, 14610–14620.

Southwest Fisheries Science Center
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Laboratory Objectives

The mission of the La Jolla Laboratory is to develop feasible options for managing Pacific coastal fisheries, world and national tuna fisheries, and marine mammal populations—options that are based on the best scientific and statistical information available. The Laboratory also estimates the biological, environmental, economic, and social impacts of these options, and provides advice for international commissions.

The La Jolla Laboratory occupies a cliff top overlooking the Pacific Ocean, next to Scripps Institution of Oceanography (SIO) on the campus of the University of California, San Diego, in La Jolla, California. Headquarters for the Southwest Fisheries Science Center, the La Jolla Laboratory employs 65 research scientists and a supporting staff of up to 75 in the conduct of multidisciplinary research programs.

Most of its research is organized under four major groups: Antarctic Ecosystem Research Group, Coastal Fisheries Resources Division, Fishery-Marine Mammal Interactions Division, and Pelagic Fisheries Resources Division.

Personnel

Izadore Barrett, Director
Richard A. Neal, Deputy Director
David J. Mackett, Program and Planning Officer
Benjamin F. Remington, Executive Officer
Rennie S. Holt, Chief, Antarctic Ecosystem Research Group
Roger P. Hewitt, Leader, Antarctic Krill Stock Assessment Program
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John R. Hunter, Leader, Coastal Eastern Pacific Population Biology of Fishes
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Pierre Kleiber, Leader, Pelagic Ecosystem Model Development Program.
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Areas of Expertise

The staff of the Coastal Fisheries Resources Division assesses the biomass of Pacific groundfishes and other valuable fish stocks, and evaluates biological and environmental factors that affect their abundance, distribution, survival, and recruitment. The Division also studies factors that affect the economics of the fisheries supported by these fishes. The work is done primarily in support of the Pacific Fisheries Management Council so that these resources can be managed effectively. The information is based on fishery-independent data on fish stocks collected by the staff on trawl and ichthyoplankton survey cruises, and fishery-dependent data gathered from other sources.

The Fishery-Marine Mammal Interactions Division is responsible for monitoring the status of dolphin populations in the eastern tropical Pacific (ETP) and the coastal marine mammals of California. Provisions of the Marine Mammal Protection Act of 1972 and later amendments guide the activities of the Division. These activities include monitoring the abundance of ETP dolphin and coastal marine mammal stocks, and assessing the impact of fishing operations on these populations. The Division's staff also develops and tests mathematical models to determine how factors such as growth, reproduction, stock interaction, and geographic distribution influence changes in population levels and our estimates of these levels. This work is also augmented by basic research on marine mammals carried out by Senior Scientist Dr. William Perrin.

The Pelagic Fisheries Resources Division provides basic fishery analysis and management information on tunas, billfishes, and other large pelagic fishes. The work supports the U.S. commitment to international management of tuna fisheries, and regional management of fisheries for billfish and other pelagic species. The staff provides technical advice to the U.S. Commissioners on the Inter-American Tropical Tuna Commission and to other U.S. officials, assesses stock condition and abundance, determines the effects of fishing on stock condition and the impacts of management decisions on the fisheries and resources, provides information on distribution and migration of sport-caught billfishes, monitors developments in tuna fisheries worldwide, and develops analytical techniques to improve the precision of fisheries assessments.

The U.S. Antarctic Marine Living Resources (AMLR) Program was transferred to the Southwest Fisheries Science Center in Fiscal Year 1988. It is a congressionally mandated program assigned to the National Marine Fisheries Service under the Secretary of Commerce in 1984. The program provides a basis for U.S. policy on the management and conservation of Antarctic living resources, and is in direct support of U.S. participation in the international effort to protect the Antarctic and its marine life under the Commission and Scientific Committee of the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR). Research cruises organized by the program staff at La Jolla are directed at gathering biological information on fish, krill, seal, penguin, and pelagic seabird populations off the northernmost tip of the Antarctic Peninsula and South Georgia, and obtaining vital physical information on Antarctic marine environment.

Laboratory Features

The Laboratory's buildings are clustered around a central courtyard and a shady grove of melaleuca trees. In addition to offices and laboratories there is an experimental seawater aquarium (9,300 square feet) with water tables and environment rooms. Computer work stations linked through a Local Area Network (LAN) and microcomputers enhanced with expanded memory boards, co-processors, and accelerators enable the scientists to cost-effectively and efficiently carry out their research mission. The library contains over 17,000 books, microfiche, and bound volumes on marine biology, fisheries, and oceanography and is enhanced and supplemented by the extensive libraries at the nearby University of California, San Diego and Scripps Institution of Oceanography.

The 171-foot research vessel, *David Starr Jordan*, has been assigned by NOAA's National Ocean Survey to the La Jolla Laboratory. Each year the *Jordan* logs about 30,000 miles conducting surveys of the fish and marine mammal resources and the oceanography of the eastern Pacific from Oregon to South of the equator. Other ships, such as the NOAA vessels *Surveyor* and *MacArthur*, are used by the Center to conduct surveys in the Pacific Ocean and Antarctic seas.

Laboratory History

The buildings of the La Jolla Laboratory were dedicated in 1964 and originally housed two federal fisheries laboratories—the Tuna Resources Laboratory and the California Current Resources Laboratory. The land associated with the newly built Fishery-Oceanography Center, as it was first known, was deeded to the federal government by the Regents of the University of California. The Tuna Resources Laboratory conducted oceanographic and biological research on the tunas of the eastern Pacific Ocean. The California Current Resources Laboratory initially examined sources of decline in the California sardine resource, then later broadened this focus to examine factors affecting abundance, distribution, and availability of various oceanic fish in the Current. This work was largely within the framework of the California Cooperative Oceanic Fisheries Investigations (CalCOFI), an interagency consortium formed in 1947 to conduct this type of research on a cooperative state-federal basis.

In 1967, these laboratories were merged to form the nucleus of what is now the La Jolla Laboratory of the Southwest Fisheries Science Center. The first director of the Center, Dr. Elbert H. Ahlstrom, was succeeded by Dr. Alan R. Longhurst the same year. In 1972, Dr. Brian J. Rothschild succeeded Longhurst as Center director, followed by the present director of science and research, Dr. Izadore Barrett, who has been in that position since 1977.

Cooperating Agencies

The scientific staff of the Center's La Jolla Laboratory has developed close links with the Scripps Institution of Oceanography and the Institute of Marine Resources of the University of California. Several Laboratory staff members have received research appointments to the University of California, San Diego, faculty as adjunct professors and research associates. Graduate students receive training and research opportunities at the La Jolla Laboratory.

Scientists from the Laboratory, from the California Department of Fish and Game, and from Scripps cooperate in the CalCOFI Program, collecting samples and data at sea on survey cruises. Scripps chiefly processes and analyzes oceanographic observations and studies the taxonomy and zoogeography of plankton organisms other than fishes, while NMFS scientists at La Jolla are responsible for the fishery biology. As a result of the CalCOFI effort, the biology and oceanography of 250,000 square miles of the Pacific Ocean off California and Baja California is perhaps the best ecologically understood of any comparable body of water in the world.

The La Jolla Laboratory has a close working liaison with the California Department of Fish and Game. Presently, the state and federal governments collaborate in research on coastal marine mammals, management of fisheries, particularly transboundary stocks such as the northern anchovy (shared with Mexico), and in the preparation of fishery resource stock assessments mandated under the Fishery Conservation and Management Act.

Scientists at the La Jolla Laboratory have developed a formal collaboration known as "MEXUS-Pacifico" with Mexico's Instituto Nacional de Pesca to obtain the best scientific information available on shared fish stocks, through cooperative research. With the Soviet Union, the La Jolla Laboratory has conducted cooperative studies of the distribution of the Pacific whiting spawning stocks off central and southern California and Baja California, a result of the Governing International Fisheries Agreement (GIFA) between the two countries.

In addition, the La Jolla Laboratory conducts research in support of the U.S. commitments to the Inter-American Tropical Tuna Commission, the International Commission for the Conservation of Atlantic Tunas, and the Commission for the Conservation of Antarctic Marine Living Resources.

Susan Smith and Lillian Vlymen

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Detecting Differences in Fish Diets

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Statistical comparison of the diet of a predator between areas or time-periods allows one to distinguish true dietary differences from sampling variability and may lead to a better understanding of a species' feeding habits. Despite the utility of statistical testing, few procedures appropriate for dietary comparisons have been developed. Perhaps one impediment to the development of a general approach to dietary comparisons is the wide variety of ways in which diets have been expressed and the lack of consensus about which is best. For example, diets expressed as the numeric or gravimetric proportions of the total food consumed will require different approaches to statistical comparison than those expressed either as the proportion of the samples containing each of the various prey types, or as the index of relative importance of each prey type (Pinkas et al. 1971).

For cases in which diets are expressed in terms of gravimetric proportions, Crow (1979) and Ellison (1979) have recommended statistical tests of between-sample differences based on multivariate analysis of variance (MANOVA). Validity of such tests, however, requires that the prey proportions have a multivariate normal distribution and that the variance-covariance structure of the prey proportions is identical among samples (Morrison 1976). Recognizing that dietary data are unlikely to have these properties, Crow (1979) further recommended using MANOVA that incorporates non-parametric procedures. Herein, this recommendation is followed, and a new approach for testing differences in diets using non-parametric MANOVA is examined. This approach combines the usual measure of between-sample differences employed in parametric MANOVA (i.e., Hotelling's T^2 statistic; Morrison 1976) and a non-parametric procedure (i.e., a randomization test; Edgington 1987) to determine the significance of T^2. The method is then applied to determine whether the diet of pelagic armorhead *Pseudopentaceros wheeleri* from the Southeast Hancock Seamount changed between two sampling periods.

Materials and methods

Testing for between-sample differences is accomplished in three steps: (1) calculating for each sample the gravimetric dietary proportions and their variances and covariances, (2) calculating a measure of the statistical difference between samples, and (3) determining the statistical significance of the measure. The gravimetric proportion of the diet contributed by prey category j(p_j) can be estimated as the total weight of prey category j in all stomach samples divided by the total weight of all prey categories combined (Hyslop 1980). Algebraically this is expressed as

$$p_j = \frac{\Sigma_k w_{jk}}{\Sigma_j \Sigma_k w_{jk}} = \frac{w_{j.}}{w_{..}} \qquad (1)$$

where w_{jk} is the weight of prey category j for individual k, $w_{j.}$ is the total weight of prey category j summed across all individuals, and $w_{..}$ is the total weight of all prey. Each p_j is transformed to x_j, where $x_j = \arcsin\sqrt{p_j}$, so that it conforms more closely to a normal random variable (Sokol and Rohlf 1969). Because x_j is estimated as a pooled proportion rather than the average of the proportions for individual fish, the variance of x_j and the covariance between x_j and x_i cannot be calculated directly and instead are approximated by using the delta method (Seber 1973). In the following, $\mathbf{x}_i$ indicates the vector of x_j for sample i, and S_i indicates the matrix of variance and covariance estimates for $\mathbf{x}_i$.

The measure of statistical difference used is the Hotelling's T^2 statistic, a multivariate extension of the t-statistic (Morrison 1976). In matrix notation, this statistic is expressed as

$$T^2 = (\mathbf{x}_1 - \mathbf{x}_2)'\, S.^{-1}\, (\mathbf{x}_1 - \mathbf{x}_2), \qquad (2)$$

where $S.^{-1}$ is the inverse of the pooled estimate of the variance-covariance matrix (Morrison 1976). S. is approximated, assuming reasonably large sample sizes (>50 stomachs with prey per sample), as

$$S. = \frac{2(N_1 S_1 + N_2 S_2)}{N_1 + N_2}, \qquad (3)$$

where N_1 and N_2 are the sizes of the two samples.

Once a value of T^2 is computed, its significance is determined from an empirical probability distribution of T^2 computed by using a technique known as randomization (Edgington 1987). Computation of the empirical probability distribution using this technique proceeds as follows: (1) stomach content data from both time or area samples are

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Table 1

Probability levels associated with the randomization tests of the individual hypotheses. Because these are *a posteriori* tests, significance levels were adjusted according to the Bonferroni inequality to 0.25α ($^{*}P\leq 0.0125$, $^{**}P\leq 0.0025$).

	Mean proportion			
	Sample 1	Sample 2	t-value	Probability level
Tunicates	0.32	0.69	−9.1	<0.001**
Crustaceans	0.27	0.13	5.0	0.011*
Fish	0.26	0.10	3.7	0.046
"Others"	0.15	0.08	1.9	0.294

combined, (2) the combined data are randomly sorted into two new samples equal in size to the originals, and (3) a value of T^2 is calculated for the two samples. Steps 2 and 3 are repeated iteratively (the present study uses 5000 iterations), and the probability distribution of the randomized values of T^2 is then calculated. Next, the significance level of obtaining the original T^2 is estimated by determining the proportion of the randomized T^2 values that, ignoring signs, is equal to or greater than the original.

If between-sample equality of the diet is rejected, it is then appropriate to test for the equality of individual prey categories to determine which categories contribute most to the difference in diet. In this case, the measure of statistical difference used is the univariate t-statistic. In matrix notation, the vector of t-statistics (**t**) can be computed as

$$\mathbf{t} = \mathbf{D}._{}^{-1}(\mathbf{x}_1 - \mathbf{x}_2), \tag{4}$$

where $\mathbf{D}.^{-1}$ is the inverse of a matrix formed from the diagonal elements of $\mathbf{S}.$. As before, the significance of each t-statistic is determined from an empirical probability distribution computed for each prey category using randomization. Computation of these probability distributions is identical to that described for the multivariate case, except that a matrix of univariate t-statistics (Eq. 4) is used in the calculation instead of the T^2-statistic (Eq. 2). These individual tests are *a posteriori* tests and require some adjustment of the error rate considered to be significant. Using the Bonferroni inequality (Morrison 1976, Miller 1981), an appropriate adjustment is to assume significance at $\alpha \cdot n^{-1}$.

The above procedures have been incorporated into the computer program DIETTEST, which is designed to run on IBM-compatible microcomputers. This program is available from the author.

As an example of the application of this method, it has been used to test for dietary differences between two samples of pelagic armorhead: 55 fish collected in June 1985, and 101 fish collected in August 1988 (only fish with prey in their stomachs were used in the analysis). Both samples were obtained from the Southeast Hancock Seamount (lat. 30°N, long. 180°W) on the Hawaiian Ridge. Stomach contents were sorted to the lowest taxonomic category possible, then blotted and weighed to the nearest milligram. To simplify the analysis, various prey items were pooled into four major prey categories: tunicates, crustaceans, fish, and "others."

Results and discussion

When the method was applied to the two armorhead samples, the test of the simultaneous equality of all dietary proportions between samples was highly significant ($P<0.001$), indicating that the diet of pelagic armorhead had changed between the two sampling periods. Because of this, tests were also made for individual prey categories. Two of the four prey categories, tunicates and crustaceans, differed significantly between samples (Table 1) and therefore appeared to be responsible for the overall difference in diet.

The measure of between-sample difference, T^2, employed in the proposed test was selected primarily because the absolute differences between samples are scaled by the within-sample variances, a particularly desirable feature when dealing with highly variable quantities such as fish diets. This choice, however, imposes a constraint on the proposed statistical test; that is, the method can only be applied to cases in which the two diet samples lack mutually exclusive components. This constraint arises because computation of T^2 requires inversion of the variance-covariance matrix (Eq. 2) which is singular and therefore not invertible when a prey category is completely absent from one of the samples. Although this constraint may not be severe when the diet of a single predator is being examined for spatial or temporal variation, especially if one is willing to accept the pooling of prey to relatively high taxa, the proposed method is likely to be of limited value for comparing the diets of different predators. For such between-predator comparisons, a more appropriate test could be developed by utilizing some measure of diet overlap (Caillet and Barry 1979) which is not affected by mutually exclusive prey categories, instead of T^2 as a measure of between-sample difference.

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Citations

Caillet, G.M., and J.P. Barry
1979 Comparison of food array overlap measures useful in fish feeding habit analysis. *In* Lipovsky, S.J., and C.A. Simenstad (eds.), Gutshop '78 fish food habits studies; Proceedings of the second Pacific Northwest technical workshop, October 10–13, 1978, Maple Valley, Washington, p. 67–79. Wash. Sea Grant Publ., Univ. Wash., Seattle.

Crow, M.E.
1979 Multivariate statistical analysis of stomach contents. *In* Lipovsky, S.J., and C.A. Simenstad (eds.), Gutshop '78 fish food habits studies; Proceedings of the second Pacific Northwest technical workshop, October 10–13, 1978, Maple Valley, Washington, p. 87–96. Wash. Sea Grant Publ., Univ. Wash., Seattle.

Edgington, E.S.
1987 Randomization tests, 2d ed. Marcel Dekker, NY, 341 p.

Ellison, J.P.
1979 The use of discriminate analysis in the study of fish food habits. *In* Lipovsky, S.J., and C.A. Simenstad (eds.), Gutshop '78 fish food habits studies; Proceedings of the second Pacific Northwest technical workshop, October 10–13, 1978, Maple Valley, Washington, p. 80–86. Wash. Sea Grant Publ., Univ. Wash., Seattle.

Hyslop, E.J.
1980 Stomach contents analysis—a review of methods and their application. J. Fish. Biol. 17:411–429.

Miller, R.G. Jr.
1981 Simultaneous statistical inference, 2d ed. Springer-Verlag, NY, 299 p.

Morrison, D.F.
1976 Multivariate statistical methods, 2d ed. McGraw-Hill, NY, 415 p.

Pinkas, L., M.S. Oliphant, and I.L.K. Iverson
1971 Food habits of albacore, bluefin tuna, and bonito in California water. Calif. Dep. Fish Game. Fish. Bull. 152, 105 p.

Seber, G.A.F.
1973 The estimation of animal abundance and related parameters. Hafner Press, NY, 506 p.

Sokol, R.R., and F.J. Rohlf
1969 Biometry. W.H. Freeman, San Francisco, 776 p.

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Bias in the Wetherall Estimates of Z/K and L_∞ Due to Population Disequilibria

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Abstract

The method of Wetherall (1986, Fishbyte 4(1):12-14) for estimating Z/K and L_∞ from length-frequency data sampled from a population in equilibrium (constant recruitment and mortality) was examined through simulation of population experiencing rapid change in recruitment and fishing mortality. The results show a large bias of Z/K and L_∞ to be generated under non-equilibrium situation; this bias cannot be removed by smoothing. However, departure from equilibrium can be detected, and hence the conditions identified where the method remains applicable.

Introduction

The regression estimator of Z/K and L_∞ developed in Wetherall et al. (1987) has recently received considerable use in cases in which the length frequencies are not multimodal or are from only a single sample (Wetherall 1986; Arellano 1989; Polovina 1989; Rawlinson 1989). This estimator is based on the assumption of an equilibrium population (i.e., a population experiencing fishing effort and recruitment that are constant). Although Wetherall et al. (1987) clearly caution potential users of the bias that may result from applying the method to populations not in equilibrium, no estimates of the likely magnitudes of such bias were provided. This prompted us to investigate the sensitivity of the method to two common types of perturbations: 1) a rapid increase in effort during the fishing-up stage of a fishery and 2) a one-year doubling of recruitment. Here we examine the bias associated with these types of disequilibria.

Assessing the Wetherall Method

Performance of the Wetherall method was assessed by applying it to catch length frequencies generated by a population simulation model. The model - which was configured to simulate a population of opakapaka, *Pristipomoides filamentosus*, a Hawaiian deepwater snapper - accounted for growth, fishing and natural mortality, size selectivity of the fishing gear, and recruitment. Simulations of a rapid increase in fishing effort started with the equilibrium length-frequency distribution that would occur in the absence of fishing. Fishing mortality was set at 0.6 year^{-1}, and the model was then run until the new equilibrium length-frequency distribution was obtained. Simulations of a one-year doubling of recruitment started with the equilibrium length-frequency distribution at a fishing mortality of 0.6 year^{-1}. Annual recruitment was doubled for one year, and the model was then run to the new equilibrium. In both cases, Z/K and L_∞ were estimated each year subsequent to the perturbation by applying the Wetherall method to the simulated catch length frequencies.

These simulations indicated that the bias in Z/K and L_∞ varies tremendously between the initial perturbation and the subsequent equilibrium. When fishing effort was increased rapidly, the bias in Z/K was initially negative, then became positive before decaying to zero (Fig. 1A). The bias in L_∞ varied similarly with time but was almost always positive and considerably smaller than that of Z/K (Fig. 1A). When recruitment was doubled for one year, the bias of Z/K was initially positive, then became negative (Fig. 1B). The bias of L_∞ varied similarly, but again was considerably smaller than that of Z/K. Although the simulated changes in fishing mortality and recruitment may be more abrupt than those typically experienced by a population, the results clearly demonstrate that disequilibrium can cause large bias in Z/K estimates.

Two possible methods for minimizing the risk of obtaining such biased estimates of Z/K and L_∞ were examined. First, we examined whether

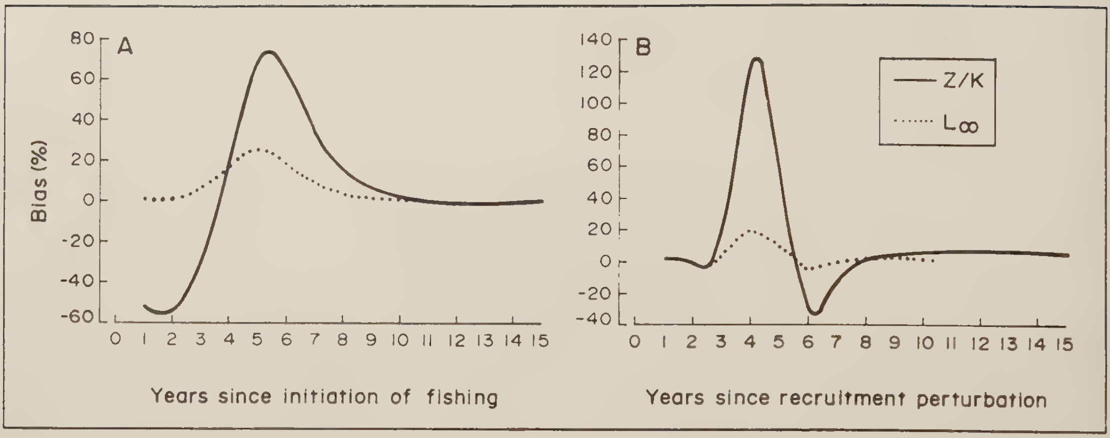

Fig. 1. Time trajectories of Z/K bias and L_∞ bias after (A) a rapid increase of fishing effort and (B) a one-year doubling of recruitment.

smoothing the length-frequency distributions by using a three-year running average before application of the Wetherall method would reduce the effects of the perturbation. The effectiveness of smoothing depended on the type of perturbation. When fishing effort was rapidly increased, smoothing had almost no effect on Z/K bias (Fig. 2A), but when recruitment was doubled, smoothing had a greater effect, especially during periods of maximum bias, when reductions in Z/K bias were up to 30% (Fig. 2B). Overall, however, the three-year smoothing appears to be an ineffective way of reducing disequilibrium bias.

Second, we examined the possibility of statistically detecting the disequilibrium conditions that lead to bias. This was done by comparing the catch length-frequency distribution in any one year to those from the previous two years by using a chi-square test of independence. The rationale for this type of test is that a population in equilibrium should produce catch length frequencies that, except for sampling variability, are identically distributed over time. Significance of the chi-square test therefore indicates that the population is not in equilibrium. The statistical power of the test was examined in a Monte Carlo experiment where the test was applied to catch length frequencies generated by the population simulation model. For each of the disequilibrium simulations, annual catch length frequencies were subsampled with replacement (N =

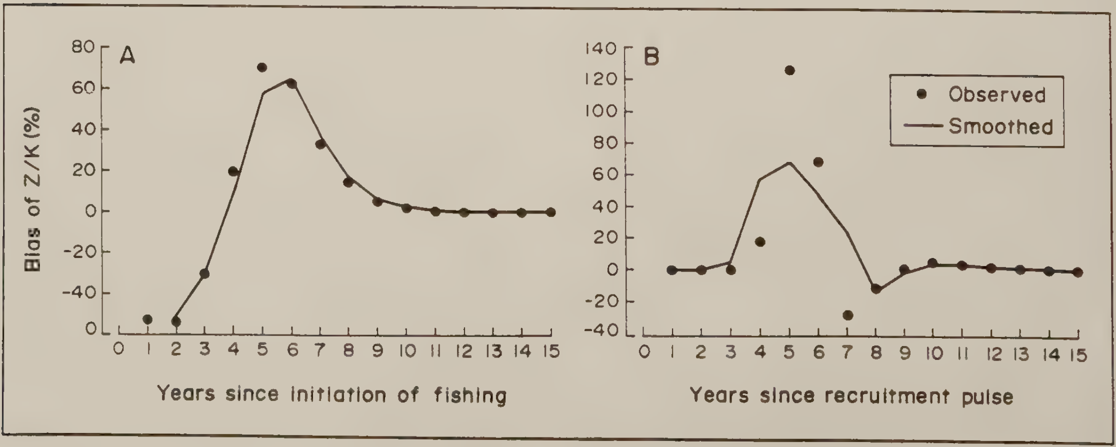

Fig. 2. Time trajectories of Z/K bias after (A) a rapid increase in fishing effort and (B) a one-year doubling of recruitment are shown before and after smoothing catch length frequencies with a three-year running average.

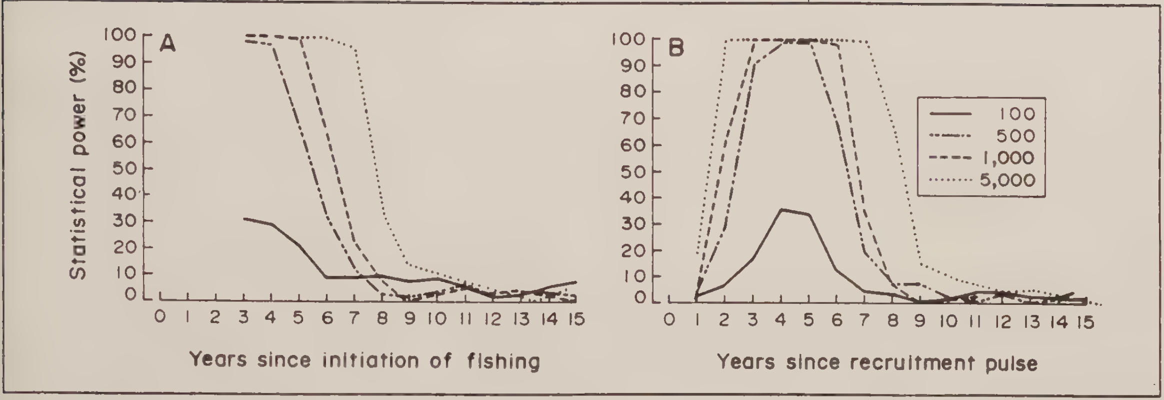

Fig. 3. Time trajectories in the statistical power of a chi-square test to detect population disequilibrium at each of four levels of sampling (N = 100; 500; 1,000; and 5,000 fish) for (A) a rapid increase in fishing effort and (B) a one-year doubling of recruitment (B).

100; 500; 1,000; 5,000 fish). At each level of subsampling, a chi-square test of independence was performed on each three-year sequence of length frequencies. Subsampling and testing were replicated 100 times, and statistical power was estimated as the proportion of the 100 tests that was significant at the 5% level.

The utility of the chi-square test in detecting conditions that likely result in biased estimates can be assessed by comparing the bias curves (Fig. 1) with the power curves (Fig. 3). For example, when fishing effort was rapidly increased and the sample size was 5,000 fish, the power of detecting disequilibria was high (i.e., >0.75) from years 3 to 7 (Fig. 3A). This indicates that, except for the first two years of the series when data were insufficient, the chi-square test had a high probability of detecting perturbations leading to Z/K bias greater than 10%. Compared with the cases of increasing effort, when recruitment was doubled for one year, power was high over a broader time period and tended to stay high with declining sample sizes (Fig. 3B). Thus, provided sample sizes are reasonably large, the chi-square test appears to be an effective way of detecting disequilibrium conditions and thereby avoiding bias.

From the foregoing, it is clear that disequilibrium bias in the Wetherall estimates of Z/K and L_∞ can be large and that averaging length frequencies over time does not remove such bias. Thus, the Wetherall method should be used with extreme caution on new or changing fisheries or species experiencing recruitment fluctuations, and in all cases, its use should be preceded by a statistical verification of population equilibrium.

References

Arellano, R.V. 1989. Estimation of growth parameters in *Panulirus penicillatus* using a Wetherall plot and comparisons with other lobsters. Fishbyte 7(2): 13-15.

Polovina, J.J. 1989. Density dependence in spiny lobster, *Panulirus marginatus*, in the northwestern Hawaiian Islands. Can. J. Fish. Aquat. Sci. 46: 660-665.

Rawlinson, N. 1989. Population dynamics of the commercially important baitfish species *Stolephorus heterolobus* in Solomon Islands. Fishbyte 7(1): 12-17.

Wetherall, J.A. 1986. A new method for estimating growth and mortality parameters from length-frequency data. Fishbyte 4(1): 12-14.

Wetherall, J.W., J.J. Polovina and S. Ralston. 1987. Estimating growth and mortality in steady-state fish stocks from length-frequency data, p. 53-74. *In* D. Pauly and G.R. Morgan (eds.) Length-based methods in fisheries research. ICLARM Conf. Proc. 13, 468 p.

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Robustness of the Wetherall Length-based Method to Population Disequilibria

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Abstract.–For fish populations in equilibrium, estimates of Z/K and L_∞ can be obtained solely from length-frequency data by using the Wetherall length-based method. Robustness of this method to departures from equilibrium conditions is examined with a population simulation model. During disequilibrium conditions following either the initiation of a fishery or a 1-year perturbation in recruitment, estimates of both parameters, especially Z/K, are severely biased. Three-year averaging of catch length-frequencies does not substantially reduce this bias. A test, based on the chi-square statistic, is proposed for detecting population disequilibrium. Provided that the sizes of length-frequency samples are sufficiently large, the test is an effective way to detect population disequilibrium and thereby avoid biased parameter estimates.

Assessments of tropical fish stocks have increasingly turned to length-based methods rather than the more traditional age-based methods, because of the difficulty in ageing tropical fishes (Pauly and Morgan 1987). Although all length-based methods use length-frequency data, they are designed to measure different biological parameters and vary in their requirements for additional types of data. Wetherall et al. (1987) examined one class of length-based methods—those designed to estimate both growth and mortality parameters without the need for additional data—and developed two new estimators: a maximum likelihood estimator and a regression estimator. The second estimator, because of its simplicity, has received the most widespread use (Wetherall 1986, Arellano 1989, Polovina 1989, Rawlinson 1989).

The regression estimator of Wetherall et al. (1987), henceforth referred to simply as the Wetherall method, estimates two parameters. The first (Θ) is the ratio of the instantaneous total mortality rate (Z) to the rate constant of the von Bertalanffy growth function (K). The second (L_∞) is the asymptote of the von Bertalanffy growth function. These parameters are estimated by regressing the mean length ($\bar{l}_i$) of all fish $\geq l_{ci}$ on l_{ci}, a cutoff length ranging from the first length category that is fully selected by the fishery (L_c) to the largest length category. Estimates of Z/K and L_∞ are then calculated as $Z/K = B/(1-B)$ and $L_\infty = A/(1-B)$, where A is the intercept and B is the slope of the regression.

Like many other length-based methods, the Wetherall method requires the population to be in equilibrium, a condition often not fulfilled because of variations in both the environment and the fishery (Csirske et al. 1987, Ralston 1989). Although Wetherall et al. (1987) clearly have cautioned potential users that biases may result if populations are in disequilibria, the likely magnitudes of such biases have not been addressed. This has prompted us to investigate the sensitivity of the method to two common types of perturbations: (1) a rapid increase in effort during the fishing-up stage of a fishery, and (2) a fluctuation in recruitment. In this paper, we examine the temporal patterns and magnitudes of biases associated with these disequilibria and present a simple statistical test that can be used with catch length-frequencies to detect population disequilibria and help minimize the consequent potential for biased parameter estimates.

Materials and methods

The performance of the Wetherall method can be assessed by applying it to catch length-frequencies generated by a length-based population simulation model that accounts for growth, mortality, and recruitment. The model is configured to

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simulate a population of opakapaka *Pristipomoides filamentosus*, a Hawaiian deepwater snapper. Mean length-at-age (L_t) is described by a von Bertalanffy growth equation:

$$L_t = L_\infty (1 - e^{-K(t-t_0)}); \tag{1}$$

where L_∞, K, and t_0 are parameters. Estimates for these parameters ($L_\infty = 66\,\text{cm}$, $K = 0.24/\text{year}$, and $t_0 = -0.78$ year) are from Ralston and Miyamoto (1983). As a computational convenience, however, growth is considered an incremental process:

$$L_t = L_1 + \sum_{i=1}^{t-1} DL_i, \tag{2}$$

where the annual growth increment (DL_t) is expressed as a time-differenced form of Equation (1):

$$DL_t = L_{t+1} - L_t = L_\infty e^{-K(t-t_0)} (1 - e^{-K}). \tag{3}$$

Variance in length-at-age (V_t) is described by an asymptotic function of age:

$$V_t = C(1 - e^{-Dt}), \tag{4}$$

where C and D are parameters. Estimates of these parameters can be obtained by fitting this function to size and age data obtained from Ralston and Miyamoto (1983), but the predicted variance is unrealistically large. Consequently, the parameters C = 10 and D = 0.1 are chosen to best fit the predicted-to-observed length-frequency distributions. Variance in annual growth increment is described as a time-differenced form of Equation (4):

$$DV_t = V_{t+1} - V_t = C(1 - e^{-D}) e^{-Dt}. \tag{5}$$

Recruitment is assumed to occur instantaneously at age-1 and, unless experimentally manipulated, to be identical each year. The length distribution of recruits is assumed to be normal with a mean and variance defined by Equations (1) and (4), respectively. The length distribution of the surviving members of this age-class in subsequent years (y) is estimated with the recursive relationship:

$$N_{l,t+1,y+1} = \sum_{s=l_0}^{l} N_{s,t,y}\, e^{-(M+QF)}\, P(l-s|t); \tag{6}$$

where M and F are the instantaneous rates of natural and fishing mortality, Q is a size-dependent selectivity coefficient, l_0 is the smallest individual in each age group and $P(l-s|t)$ is the conditional probability of growing an amount $(l-s)$ at t years of age. The growth-increment probability function is assumed to be normal with a mean and variance computed from Equations (3) and (5). An estimate of natural mortality (M = 0.3) is obtained from Ralston (1987); estimates of fishing mortality (F = 0.3 and 0.6) are chosen somewhat arbitrarily to bracket the probable true value for opakapaka. The selectivity coefficient Q is represented by a reparameterized logistic function of length:

$$Q = \frac{1}{1 + e^{-E(l-l_{50})}}, \tag{7}$$

where E is a parameter controlling the steepness of the function, and l_{50} is a parameter controlling the length of 50% selectivity. The parameter values of E = 0.5 and $l_{50} = 45\,\text{cm}$ are chosen arbitrarily. The population length-distribution is calculated by summing across all age-classes, i.e.,

$$N_{l,\cdot,y} = \sum_t N_{l,t+1,y}, \tag{8}$$

and the catch length-frequency distribution is calculated as

$$C_{l,\cdot,y} = N_{l,\cdot,y} \left(\frac{QF}{M+QF}\right) (1 - e^{-(M+QF)}). \tag{9}$$

The parameters Z/K and L_∞ are estimated from the simulated catch length-frequency distribution as follows. First, the length at full vulnerability (L_c) is estimated as one length interval (1 cm) larger than the rightmost mode in the catch length-frequency distribution (Polovina 1989). Second, $\bar{l}_i$, the mean length of all fish $\geq l_{ci}$, is calculated for each $l_{ci} > L_c$. Third, $\bar{l}_i$ is regressed on l_{ci} by using weighted linear regression with weights equal to the sample size (i.e., ΣC_l for $l > l_c$). Fourth, Z/K and L_∞ are then computed from the previously specified functions of the regression coefficients.

The disequilibrium experiments are conducted as follows. For the experiments examining the fishing-up phase of a fishery, the initial population length-frequency distribution is set at the equilibrium distribution in the absence of fishing. This length distribution is generated by running the model with F = 0.0 until the population is in equilibrium (i.e., until the total population size is identical on two successive iterations). Fishing mortality at each of the two specified levels is then applied instantaneously, and the simulation is run until the population is again at equilibrium. For the experiments examining the effect of perturbation during recruitment, the initial population length-frequency distribution is set at the equilibrium distribution with a fishery producing F = 0.6. Two types of recruitment perturbations are tested: (1) a year with twice the normal recruitment, and (2) a year with a complete absence of recruitment. After each recruitment perturbation is introduced, the simulation is run until the population is again in equilibrium. Since disequilibrium bias may be only one component of the total bias of a parameter, the disequilibrium bias is isolated by expressing it as a percentage difference relative to the equilibrium value rather than the known value of a parameter.

Population equilibrium is statistically tested by comparing a catch length-frequency distribution in any one year to those from the previous two years by using a chi-square test of independence. Rationale for this type of test is that a population in equilibrium should, except for sampling variability, produce catch length-frequencies that are identically distributed over time. Significance of the chi-square test therefore indicates that the population is not in equilibrium. Performance of the chi-square test first requires the construction of 3-by-N frequency tables, where N is the number of size categories that are jointly defined over the 3-year sequence. To do this, the largest and smallest size categories in the catch containing at least five individuals in each of the three years are determined. Then for each year, all size categories less than the lower bound of the joint interval are pooled, as are all size categories greater than the upper bound. Once the table is constructed, the chi-square test can be performed according to the procedures described in Conover (1971).

The statistical power of the test is examined in a Monte Carlo experiment in which the test is applied to catch length-frequencies generated by the population simulation model. For each disequilibrium experiment, annual catch length-frequencies are subsampled, with replacement, with subsample sizes of 100, 500, 1000, and 5000 fish. At each level of subsampling, a chi-square test of independence is then performed on each 3-year sequence of subsampled length-frequencies. Subsampling and testing are replicated 100 times, and the power is estimated as the proportion of the 100 tests that is significant at the 5% level.

To determine whether disequilibrium bias could be reduced by averaging a series of catch length-frequencies over time, the Wetherall method is also applied to simulated catch length-frequencies after they have been time-averaged. First, the catch length-frequencies for each year are converted to proportions by length. Second, the time-series of catch proportions for each size interval is smoothed by using a 3-year centered running average. Third, the smoothed catch proportions at length for each year are then multiplied by the actual catch (in numbers) for that year to recover the true sample size.

In addition to disequilibrium bias, also examined are two types of bias that can influence Wetherall estimates of Z/K and L_∞ even when the population is in equilibrium. The focus of this examination is on the variation in these biases as a function of the chosen value of L_c. To do this, the model first is run until equilibrium conditions are reached. Then for each chosen value of L_c, the Wetherall method is applied to the catch length-frequency distribution, which experiences size selection by the fishery, and to the population length-frequency distribution. Type I bias in the estimates of Z/K is expressed as the percentage difference between the estimates based on catch length-frequencies and those based on population length-frequencies. Type II bias in the estimates of Z/K is expressed as the percentage difference between the estimates based on population length-frequencies and the known values of Z/K.

Results and discussion

As Wetherall et al. (1987) have cautioned, population disequilibrium indeed leads to biased estimates of Z/K and L_∞, but the temporal pattern and magnitude of this bias vary greatly with the type of equilibrium perturbation. In the fishing-up experiment, disequilibrium bias in the estimates of Z/K is initially large and negative, but later becomes positive before decaying to zero (Fig. 1a). Increasing the fishing mortality rate increases the magnitude of the positive bias and shortens the time in which the maximum positive bias is reached. The magnitude of fishing mortality, however, appears to have little effect on the magnitude of the initial negative bias. Disequilibrium bias in the estimates of L_∞ changes with time and with fishing mortality rate in a manner similar to the bias in Z/K, but the bias in L_∞ is almost always positive and considerably smaller than the bias in Z/K (Fig. 1b). In the recruitment perturbation experiment, when recruitment is doubled for 1 year, the disequilibrium bias in the estimates of Z/K is oscillatory in time and has a pronounced positive peak and a less-pronounced negative peak (Fig. 1c). When recruitment is eliminated for 1 year, the disequilibrium bias in Z/K is again oscillatory, but the positive and negative peaks occur 2 years later and the magnitude of the bias, especially that of the negative bias, is smaller. Disequilibrium bias in L_∞ varies with time in a manner similar to the bias in Z/K, but again the bias is smaller in magnitude (Fig. 1d). Thus, the following two points emerge from these simulations: (1) Biases in both parameters can be large but vary tremendously as the size structure of the

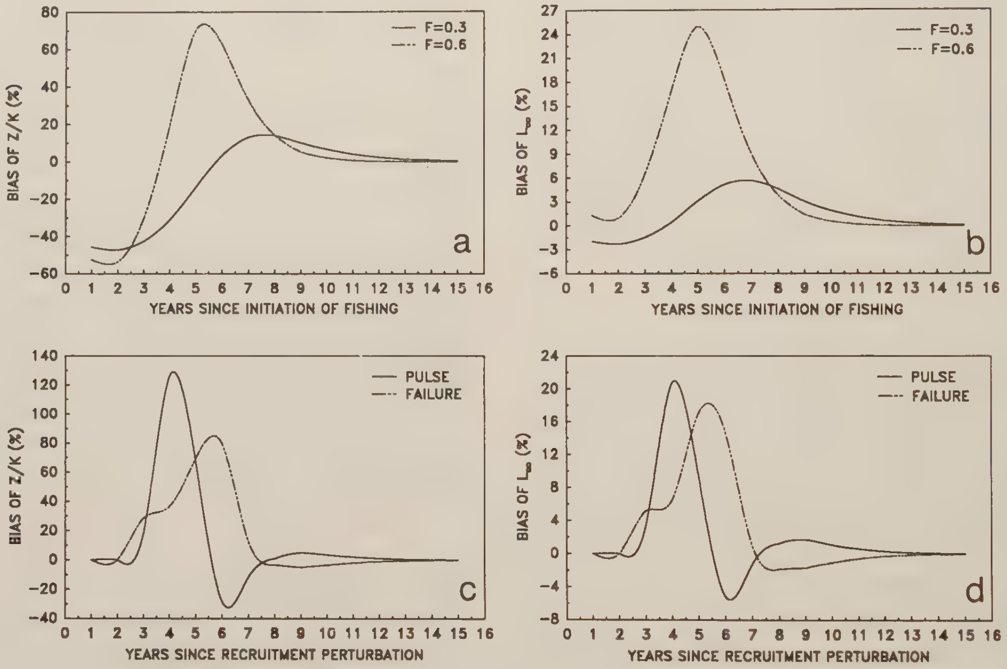

Figure 1

Temporal patterns of disequilibrium bias in the estimates of Z/K and L_∞, expressed as percentage differences relative to the equilibrium values. For the fishing-up experiment at two fishing mortality rates (F = 0.3 and 0.6), biases of (a) Z/K and (b) L_∞ are plotted against the number of years since the initiation of the fishery. For the recruitment perturbation experiment at F = 0.6, biases of (c) Z/K and (d) L_∞ are shown plotted against the number of years since a 1-year doubling of recruitment (pulse) and a 1-year absence of recruitment (failure).

population adjusts from one equilibrium to the next, and (2) bias in Z/K estimates is considerably larger than bias in L_∞ estimates.

Even though the simulated changes in fishing mortality and recruitment may be more abrupt than those typically experienced by the population, the simulations clearly demonstrate that the Wetherall estimates of Z/K and L_∞ can be quite biased when the population is not in equilibrium. As a consequence, the method apparently can be used with confidence only when population equilibrium can be demonstrated. Such a demonstration of equilibrium, or lack thereof, can be achieved by comparing successive catch length-frequencies with a chi-square test of independence. The utility of the chi-square test can best be judged by examining its statistical power to detect the disequilibrium conditions that lead to biased parameter estimates. Since the statistical power of the proposed test will increase as between-year differences in catch length-frequencies increase, it will tend to vary positively with the magnitude of parameter bias. Provided that sample sizes are sufficiently large, the test can therefore be used as a data screening device to detect when parameter bias is likely. One important consideration, then, is the relationship between sample size and the undetectable level of disequilibrium bias. This relationship can be seen by comparing the time trajectories of power (Fig. 2) with those of bias (Fig. 1).

Consider first the fishing-up experiment and bias in estimates of Z/K. For F = 0.3 and a sample size of 5000 fish, the statistical power of detecting disequilibria is high (i.e., ≥0.75) from years 3 to 7 (Fig. 2a). Although this interval includes most of the period in which bias is high (Fig. 1a), it does not include the first 2 years after the initiation of the fishery when bias is also high, because the proposed test requires 3 successive years of data. Furthermore, the interval of high statistical power does not include years 8–10 when bias is nearly

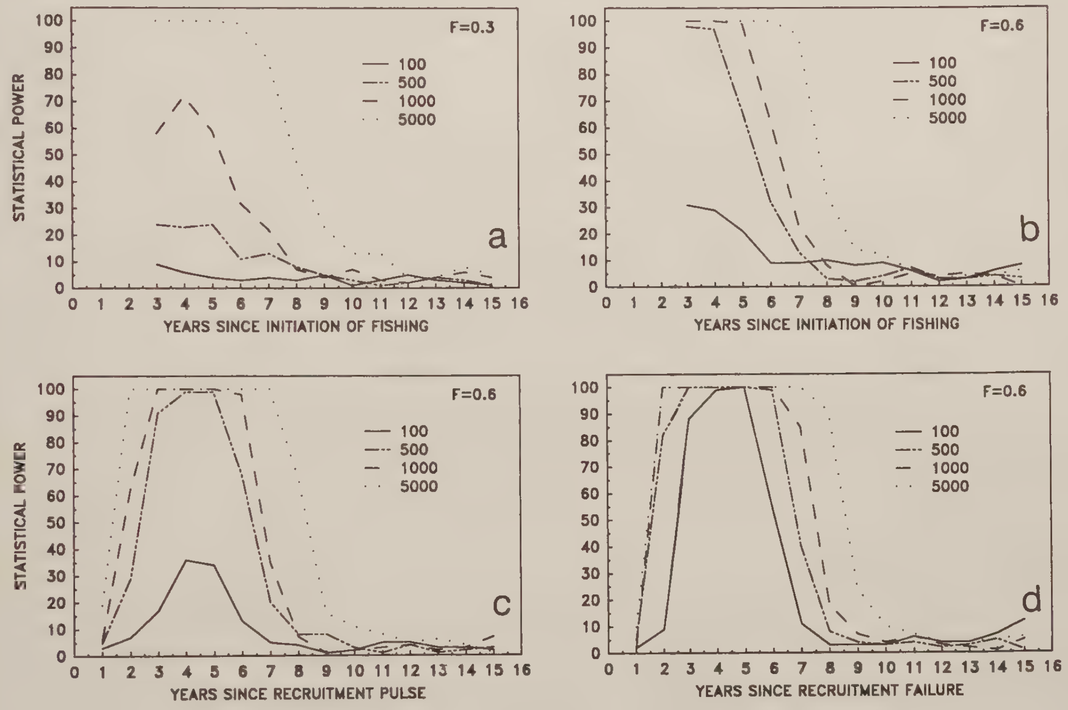

Figure 2

Temporal patterns in the statistical power of a chi-square test to detect population disequilibrium at each of four levels of sampling (N = 100, 500, 1000, and 5000). For the fishing-up experiment, power is shown for (a) F = 0.3 and (b) F = 0.6, starting in the third year after the initiation of the fishery and continuing to equilibrium. For the recruitment perturbation experiment at F = 0.6, power is shown for (c) the 1-year doubling of recruitment and (d) the 1-year absence of recruitment starting in the year in which the perturbation occurred and continuing to equilibrium.

13%. For F = 0.6 and a sample size of 5000 fish, the interval of high power is almost identical to that at F = 0.3. At lower sample sizes, however, the chi-square test is considerably more powerful when F = 0.6 than when F = 0.3.

In the recruitment perturbation experiment, statistical power is high over a broader time-interval than in the fishing-up experiment. For the case of a 1-year doubling of recruitment at a sample size of 5000 fish, power is high between years 2 and 8, an interval that includes the entire period in which disequilibrium bias is >5%. For the case of a 1-year absence of recruitment, power is high between years 2 and 8, an interval that again includes the entire period in which disequilibrium bias is >5%. Unlike the situation in the fishing-up experiments, power tends to remain relatively high with reductions in sample size. These experiments indicate that, in terms of its ability to detect the likelihood of disequilibrium bias, the chi-square test performs best on a 1-year doubling of recruitment, second best on a 1-year absence of recruitment, and worst on the fishing-up disequilibrium. The fishing-up case is worst because the test cannot be applied to the first 2 years of the time-series when bias is high and larger sample sizes are needed to detect disequilibrium.

In addition to the type of disequilibrium perturbation and size of the length-frequency sample used, the statistical power of the chi-square test also varies with the number of length-distributions included. Thus, power is calculated for tests including two, three, and four length-distributions. Since the gain in power is substantial when the number of length-distributions is increased from two to three but only minor when the number is increased from three to four, all further power simulations are based on three length-distributions.

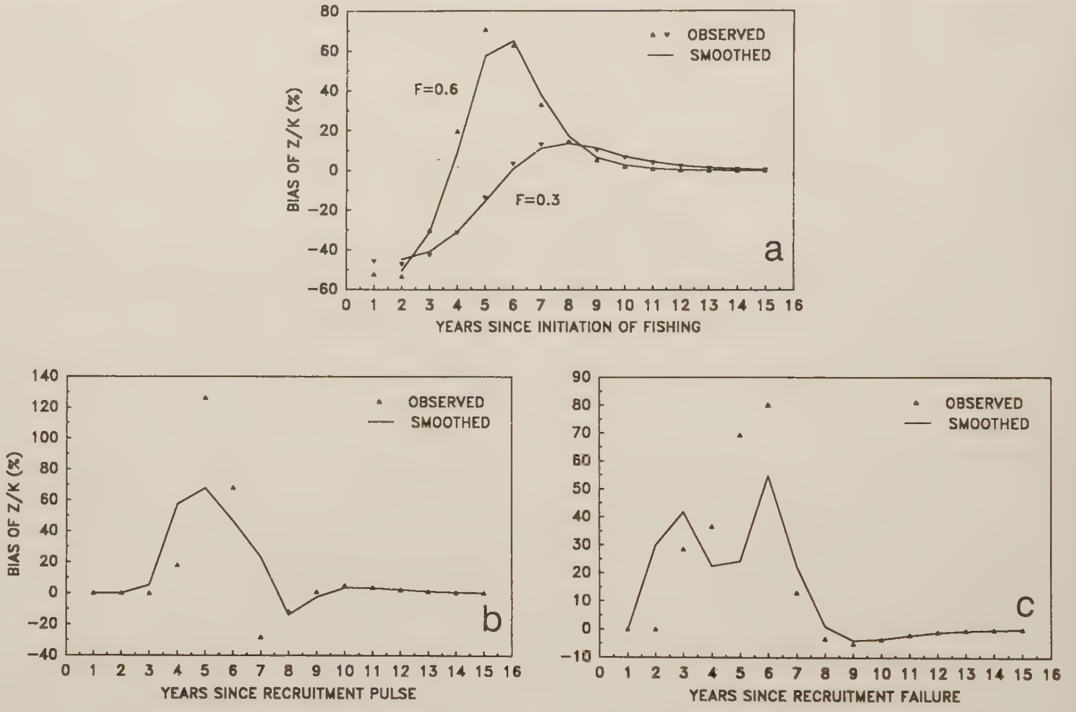

Figure 3

Effect of time-averaging catch length-frequencies, with a 3-year running average, on the bias in Z/K. (a) For the fishing-up experiment at F = 0.3 and F = 0.6, Z/K estimates based on averaged data and those based on unaveraged data are plotted against years since the initiation of the fishery. For the recruitment perturbation experiment at F = 0.6, Z/K estimates from averaged and unaveraged data are plotted against the number of years since (b) a 1-year doubling of recruitment and (c) a 1-year absence of recruitment.

If a population is found to be in disequilibrium, one can either discard the parameter estimates or find some means to reduce or eliminate the disequilibrium bias. Following the second approach, we have examined the utility of a technique often used with such age-based procedures as catch curve analysis to reduce the effects of year class variability. This technique consists of averaging the catch length frequencies over time. The effectiveness of time-averaging depends on the type of perturbation that creates the disequilibrium. In the fishing-up experiment, time averaging has essentially no effect when F = 0.3 and only a slight effect when F = 0.6 (Fig. 3a). In the recruitment variation experiment, time averaging has a somewhat greater effect, especially during the periods of maximum bias when reductions in bias are as much as 30% (Fig. 3b). Time averaging, however, also increases bias during some periods. Although time averaging is somewhat more effective when disequilibrium is due to recruitment perturbation, the 3-year time averaging employed in our study appears to be an ineffective way of reducing disequilibrium bias.

Besides disequilibrium bias, the Wetherall method is subject to two types of biases that may occur even when the population is in equilibrium. The first type of equilibrium bias (herein referred to as Type I or selection bias) is always negative and occurs when fish, equal in length to the smallest l_c values used in the regression, are not fully vulnerable to the fishery (Fig. 4a). Since, in practice, the exact form of the fishery selection curve will rarely be known, choice of the initial l_c value is somewhat arbitrarily based on the shape of a catch length-frequency histogram. Our approach follows Polovina (1989) in choosing the initial l_c to be one size-interval greater than the rightmost mode on a length-frequency histogram. This choice, however, can result in selection bias. For example, when F = 0.3, the initial l_c (51 cm) is identical to the length of 95%

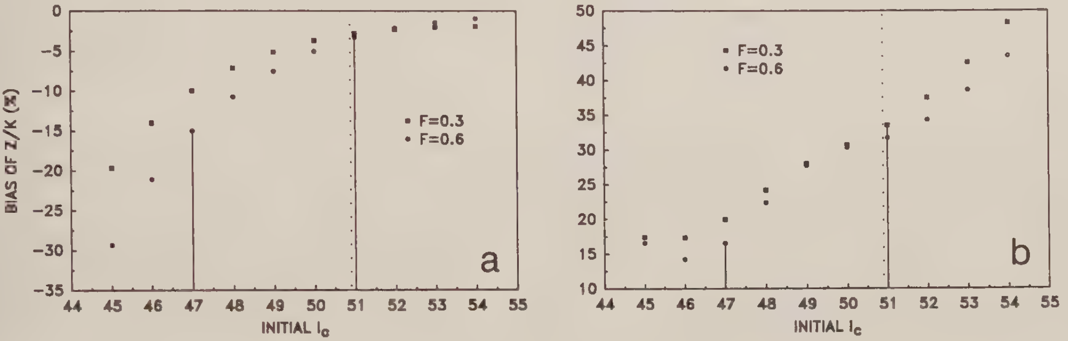

Figure 4

(a) Selection bias (i.e., bias due to inclusion in the Wetherall method of fish lengths that are incompletely selected by the fishery) and (b) residual bias (i.e., equilibrium bias that cannot be explained by selection) are shown as functions of the initial value of l_c. The l_c values (calculated as one size-interval larger than the rightmost mode in the catch length-frequency distribution) are shown as solid vertical lines at 47 cm for F = 0.6 and at 51 cm for F = 0.3. The size of 95% selection is shown with a vertical dotted line at 51 cm.

selection, and selection bias is small (3%). But when F = 0.6, the initial l_c (47 cm) is considerably less than the size at 95% selection, and selection bias is consequently larger (15%).

Since selection bias asymptotically approaches zero with increasing value of the initial l_c (Fig. 4a), one logical way of reducing equilibrium bias would be to choose a larger initial l_c. This strategy, however, would increase the second type of equilibrium bias (herein referred to as Type II or residual bias), because residual bias increases with initial l_c (Fig. 4b). For example, when F = 0.6 and the initial l_c = 47 cm, residual bias is about 16%. But when F = 0.3 and l_c = 51 cm, residual bias is 34%. Although the causes of residual bias are unknown, it could be related to either of two factors. First, as Wetherall et al. (1987) demonstrate, the estimates of Z/K and L_∞ are asymptotically unbiased as the sample size increases. Since increasing the size of the initial l_c reduces sample size, it follows that bias will increase. Second, as Laurec and Mesnil (1987) demonstrate, individual variability in growth, which has been incorporated into our simulation model, leads to bias in length-based estimates of mortality.

In the foregoing, we have demonstrated that disequilibrium bias in the Wetherall estimates of Z/K and L_∞ can be large and that time averaging does not remove such

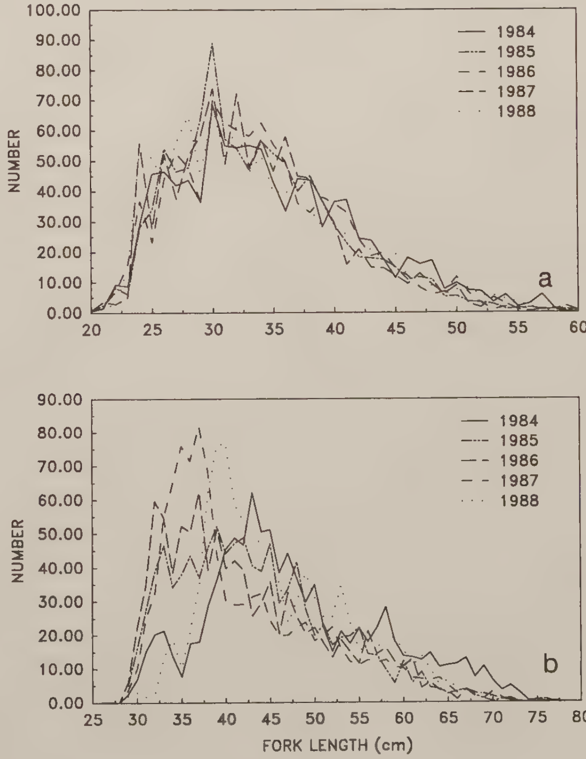

Figure 5

Catch length-frequency distributions for (a) ehu and (b) opakapaka based on 3000 fish samples collected in each year (1984–88).

bias. In light of this, the general utility of the Wetherall method clearly depends upon whether fish populations actually reach equilibrium, or conditions close enough to equilibrium, so that the consequent bias will be small. We believe, however, that equilibrium conditions may prevail more frequently than generally perceived. For example, ehu *Etelis carbunculus*, another deepwater snapper caught by Hawaii's bottomfish fishery, displays considerably less variability in size between years than opakapaka. Chi-square tests, performed on annual length-frequency samples of 3000 fish collected in 1984–88 (Fig. 5), are always not significant for ehu (1986, $P=0.19$; 1987, $P=0.40$; 1988, $P=0.11$) but are always highly significant for opakapaka (1986–88, $P<0.001$). Therefore, the ehu population is apparently close enough to equilibrium that using the Wetherall method would be appropriate. In general, however, the Wetherall method should be used with extreme caution on new or changing fisheries or species experiencing recruitment fluctuations. In all cases, its use should be preceded by a statistical verification of population equilibrium.

Citations

Arellano, R.V.
1989 Estimation of growth parameters in *Panulirus penicillatus* using a Wetherall plot and comparisons with other lobsters. Fishbyte 7(2):13–15.

Conover, W.J.
1971 Practical nonparametric statistics. John Wiley, NY, 462 p.

Csirske, J., J.F. Caddy, and S. Garcia
1987 Methods of size-frequency analysis and their incorporation in programs for fish stock assessment in developing countries: FAO interest in receiving advice. *In* Pauly, D., and G.R. Morgan (eds.), Length-based methods in fisheries research, p. 1–6. ICLARM Conference Proceedings 13, International Center for Living Aquatic Resources Management, Manila, Philippines, and Kuwait Institute for Scientific Research, Safat, Kuwait.

Laurec, A., and B. Mesnil
1987 Analytical investigations of errors in mortality rates estimated from length distributions of catches. *In* Pauly, D., and G.R. Morgan (eds.), Length-based methods in fisheries research, p. 239–282. ICLARM Conference Proceedings 13, International Center for Living Aquatic Resources Management, Manila, Philippines, and Kuwait Institute for Scientific Research, Safat, Kuwait.

Pauly, D., and G.R. Morgan (editors)
1987 Length-based methods in fisheries research. ICLARM Conference Proceedings 13, International Center for Living Aquatic Resources Management, Manila, Philippines, and Kuwait Institute for Scientific Research, Safat, Kuwait, 468 p.

Polovina, J.J.
1989 Density dependence in spiny lobster, *Panulirus marginatus*, in the Northwestern Hawaiian Islands. Can. J. Fish. Aquat. Sci. 46:660–665.

Ralston, S.
1987 Mortality rates of snappers and groupers. *In* Polovina, J.J., and S. Ralston (eds.), Tropical snappers and groupers: Biology and fisheries management, p. 375–404. Westview Press, Boulder.
1989 Effect of seasonal recruitment on bias of the Beverton-Holt length-based mortality estimator. Am. Fish. Soc. Symp. 6:190–197.

Ralston, S., and G.T. Miyamoto
1983 Analyzing the width of daily otolith increments to age the Hawaiian snapper, *Pristipomoides filamentosus*. Fish. Bull., U.S. 81:523–535.

Rawlinson, N.
1989 Population dynamics of the commercially important baitfish species *Stolephorus heterolobus* in Solomon Islands. Fishbyte 7(1):12–17.

Wetherall, J.A.
1986 A new method for estimating growth and mortality parameters from length-frequency data. Fishbyte 4(1):12–14.

Wetherall, J.A., J.J. Polovina, and S. Ralston
1987 Estimating growth and mortality in steady-state fish stocks from length frequency data. *In* Pauly, D., and G.R. Morgan (eds.), Length-based methods in fisheries research, p. 53–74. ICLARM Conference Proceedings 13, International Center for Living Aquatic Resources Management, Manila, Philippines, and Kuwait Institute for Scientific Research, Safat, Kuwait.

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Production Quota in Multiproduct Pacific Fisheries*

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Assessing the individual firm's technology and costs in a multispecies fishery allows design of a more effective output quota prior to regulation by anticipating and controlling for the firm's regulation-induced responses. An empirical study of a Pacific coast trawl fishery indicates that the firm's flexibility of product decision is tightly constrained by its technology and cost structure. Hence, as the resource stock for the regulated species, sablefish, deteriorates and the trip quota progressively tightens, the firm cannot sufficiently reorganize its product bundle to preclude increasingly large sablefish disposal. This defeats the purpose of the production quota. © 1991 Academic Press, Inc.

1. INTRODUCTION

Quotas on individual outputs are often used to regulate production flows of individual firms in multispecies (multiproduct) fisheries. In response to a quota, firms attempt to reorganize the mix and volume of the other species (outputs). If only limited changes are possible, production in excess of quota may be discarded, creating technically inefficient production and unnecessary fish mortality. Alternatively, when the mix and volume of other species produced are easily changed, these resource stocks may be threatened by excess production. Over a longer time period, output quotas can also induce changes in the quantities of quasi-fixed factors and further reduce production.

The competitive multispecies firm's regulation-induced reorganizations of its optimum output bundle depend upon the firm's technology and cost structure. Hence, tailoring quota design to technology and costs anticipates many quota-induced economic responses and allows design of a more effective quota.

Empirical studies of output quantity controls for the competitive multiproduct firm in a certain and static environment have usually been retrospective, analyzing

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comparative statics in a post-regulatory regime [13, 15]. Kirkley and Strand [7] and Squires [21] considered some of these issues when all outputs were unregulated and hence decision variables, but they did not consider the issue of the competitive firm's economic response to output regulation, and did not explicitly consider quotas.

This paper addresses the design of a command-and-control output quota which is consistent with the currently unregulated, revenue-maximizing multispecies firm's technology and cost structure when all outputs are decision variables. The emphasis is upon the firm's initial response to quota. We assess the competitive firm's reorganization of its optimum product bundle and changes in its quasi-fixed factor in response to a binding output quota. We examine the firm's short-run response to the output quota over a time period sufficiently short to assume that the abundance of the resource stock remains effectively constant and the capital stock does not adjust to its optimum full static equilibrium level; a longer-run analysis requires a more detailed bioeconomic model.

A multispecies trawl fishery off the Eureka, California area offers a case study.[1] A command-and-control quota on the quantity of sablefish landed at port for each vessel's fishing trip regulates production flows in the deep-water fishery of the continental slope for sablefish. The goals are to prevent overproduction, conserve the resource stock, maintain a year-round fishery, and enhance economic rent. The paper finds that limited flexibility to reorganize the mix and volume of outputs in response to the sablefish quota induces discards of excess production and precludes effective use of a command-and-control quota as a management tool.

Section 2 discusses the approach and methodology. Section 3 relates output quotas to the firm's technology and cost structure; additional detail is placed in the Appendix. Section 4 discusses the data, the model, and the empirical results. The final section contains concluding remarks.

2. THE APPROACH AND METHODOLOGY

The analysis assumes that unregulated firms maximize profit in two stages. In the first stage, a fishing trip, vessel operators choose their revenue-maximizing output bundle given fixed inputs, weather and resource abundance constraints, and relative product prices. Inputs on the vessel are largely fixed during a trip due to the short production period of 1 to 5 days and boats are away at sea where input levels cannot be readily changed. In this first stage, revenue-maximizing vessels are in partial equilibrium, i.e., firms maximize revenues conditional upon the quasi-fixed factors.

The input bundle can be specified as a single, composite input, since vessel size or capital stock is fixed at the trip level and largely determines the level of other inputs. The services of some inputs (particularly fuel) may vary with time at sea during an individual fishing trip, but the time at sea varies only slightly and the variation is not systematic. Revenue maximization subject to a single quasi-fixed input appears to be a reasonable assumption for a multispecies fishing firm making output decisions over such a short production period [6, 7].[2] This composite input is called effort, following the fisheries literature.

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[1] The region includes Eureka and Crescent City in California and Brookings in Oregon. Otter trawlers drag a net, then haul in the net, dump and sort the catch on deck, and store it below.

In the second stage of production, over a time period varying roughly between 3 to 14 months, fishing firms adjust the level of effort to minimize their production costs by selecting the optimal vessel size or capital stock. This paper's focus is upon the first stage of production.

The revenue function provides a duality-based approach to examine the underlying short-run production technology when, in the first stage of production, the firm is free to choose its revenue-maximizing output bundle with the composite input quasi-fixed. The revenue function provides the maximum revenue for the given level of the composite input, product prices, state of technological knowledge, and technical constraints to production. The revenue function was developed by McFadden [14], and the specialized form with a single composite input was introduced by Diewert [4]. The revenue function for a single, composite input Z is defined by $R[P; Z] = \max_Y\{P'Y : Y \in L(Z)\}$, where Y is an $M \times 1$ vector of endogenous products with a vector of competitive, exogenous prices P; $'$ is the transpose operator; and $L(Z)$ represents the firm's output possibilities set when all factors are fixed but products are decision variables. Regularity conditions are given by McFadden [14] and Sakai [19].

A nonhomothetic generalized Leontief revenue function models the revenue-maximizing vessel-level production process for an unregulated fishing trip [6, 7],

$$\begin{aligned} R[P;Z] = {} & \sum_i \sum_j A_{ij}(P_iP_j)^{1/2} Z + \sum_i A_i P_i Z^2 \\ & + \sum_i \sum_k B_{ik} D_k P_i Z + \sum_i \sum_l G_{il} E_l P_i Z, \end{aligned} \tag{1}$$

where $R(P; Z)$ is the revenue function, P_i is the product price of species i, Z is the composite input, D_k is the kth of two home port dummy variables for Brookings and Crescent City, and E_l is the lth of three quarterly dummy variables for winter, spring, and fall. The base case accounts for Eureka in the summer. The area dummy variables account for spatial variations in access to fish stocks, species abundance, and port effects on prices. The quarterly dummy variables G account for intertemporal variations in the technological constraints of weather and resource abundance.

Hotelling's Lemma gives input-compensated supply functions for unregulated production $Y(P; Z)$ [14]:

$$\begin{aligned} \delta R[P;Z]/\delta P_i = Y_i(P;Z) = {} & A_{ii}Z + A_iZ^2 + \sum_k B_{ik}D_kZ \\ & + \sum_l G_{il}E_lZ + \sum_j A_{ij}[P_j/P_i]^{1/2}Z. \end{aligned} \tag{2}$$

Symmetry is imposed by $A_{ij} = A_{ji}$, i not equal to j. Zero homogeneity in prices follows from the Generalized Leontief form.

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[2] Formally, Leontief input separability is assumed, where input quantities move in fixed proportions over time.

The input-compensated supply functions for unregulated production, Eq. (2), were estimated for vessels of at least 75 gross registered tons (GRT) which landed at least 1,000 pounds of sablefish in 1984. Catch and landings were equal and there was no quota-induced disposal at sea because 1984 was the last unregulated year (without quota). We considered only vessels with a high-speed winch allowing them to exploit a deep-water continental slope fishery concentrated on Dover sole, thornyheads, and sablefish. This fishery is centered in the area studied. Several other species were also harvested to utilize excess hold capacity and enjoy product diversity. Six species or outputs were specified: Dover sole, thornyheads, sablefish, other flatfish, other rockfish, and a residual, all others. There were 444 observations (fishing trips) on 14 vessels, with an unequal number of observations for each vessel.

3. OUTPUT QUOTAS AND THE STRUCTURE OF COST AND TECHNOLOGY

Effective quotas for regulating multiproduct firms require information on the structure of technology and costs. In this section, we discuss technical and economic characteristics specific to multiproduct production with significant implications for imposing output quotas on multiproduct firms.

3.1. Technology Tests

The form of the production technology can be assessed by likelihood ratio tests of various hypotheses. The final form of the technology has important ramifications for regulation [6, 7, 21].

Input–output separability. Separability between inputs and the M outputs implies no specific interaction between any one output and any one input [9]. The technology can then be specified as a single composite output and a single composite input. Only the levels of the catch and effort require regulation, and regulation of the species (input) mix does not adversely affect the optimal factor (product) combinations [7, 21]. If the technology is separable between outputs and the fixed input, the Generalized Leontief revenue function with one input is separable in P and Z, i.e., $R[P; Z] = R[P]Z$ [7]. The marginal rates of transformation of all output pairs are independent of factor intensities [5].[3] The econometric restriction is $A_i = 0$, $i = 1, \ldots, M$.

Jointness-in-inputs. A production process joint in inputs requires all inputs to produce all outputs. When production is nonjoint in inputs, separate production functions exist for each output or set of outputs. Hence, each production process can be separately regulated without affecting production of the other processes because there are no technological or cost tradeoffs between the output of one process and that of another [7, 21]. Nonjointness in inputs over all species implies that the Generalized Leontief revenue function with a single input is written [7]: $R[P; Z] = \Sigma_i R_i[P; Z]$. Producers maximize outputs; i.e., the supply of each species is perfectly inelastic and is determined by the production function. The required econometric restriction over all species is [7] $\delta^2 R[P; Z]/\delta P_i \delta P_j = 0$, which gives $A_{ij} = 0$, i not equal to j, all i, j. Nonjointness-in-inputs for an individual output, say Y_1, requires $A_{1j} = 0$, all j, j not equal to 1.

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[3] Since the partition is limited to two subsets, weak and strong separability are equivalent restrictions.

3.2. *Product Supply and Effort Elasticities*

The technological constraints to adjustments in output mix and volume when competitive firms respond to the output quota can be assessed for the final form of the unregulated technology by the own- and cross-price elasticities of supply. When calculated from $R[P; Z]$, these elasticities are input-compensated, because only pure substitution effects along a given product transformation frontier for a fixed input bundle are measured [19]. These elasticities are given by $E_{ij}^{\mathrm{PE}} = \delta \ln Y_i(P; Z)/\delta \ln P_j$. These trip-level elasticities will be smaller in absolute value than those over a longer time period because of Le Chatelier's principle.

When outputs are short-run complements, $E_{ij}^{\mathrm{PE}} > 0$; only the most easily regulated output requires regulation to reduce output levels. In contrast, unexpected product transformations are possible if outputs are substitutes, in which $E_{ij}^{\mathrm{PE}} < 0$, so that more than one output may require regulation.

The firm may also adjust its level of effort in response to quota. This response (not necessarily to the optimal long-run equilibrium level) can be assessed by the partial equilibrium elasticity of effort with respect to individual output prices: $E_{Zi}^{\mathrm{PE}} = \delta \ln Z/\delta \ln P_i$.

The proportional effect upon the supply of species Y_i for a proportional change in effort is given by the product-specific scale elasticity [6]: $E_{YZ}^{\mathrm{PE}} = \delta \ln Y_i/\delta \ln Z$.

3.3. *Multiproduct Costs*

The revenue function also embodies information on the shadow cost structure of a multiproduct firm. This shadow cost structure is important for examining the effects of an output quota, because the firm's regulatory-induced economic response can depend upon these costs.

The firm's total shadow cost equation is $C^*[W^*(P; Z), Y(P; Z)] = W^*Z$, where $\delta R[P; Z]/\delta Z = W^*(P; Z)$, i.e. the shadow price of Z or the marginal revenue with a one unit increase in Z [9].[4] This cost in terms of marginal revenue with a change in Z is the appropriate economic cost for the revenue-maximizing firm.[5] This opportunity cost is the revenue foregone. In addition, if the shadow price of Z (W^*) equals the market rental (W) price, then the firm's total shadow cost equals the total full equilibrium cost. $C^*[W^*(P; Z), Y(P; Z)] = C[W, Y(P, W)]$, i.e., $W^*Z = WZ^*(P, W)$, where $Z^*(P, W)$ is the full static equilibrium level of Z. The Appendix provides further details and derivations.

Economies of scope. An important component of the multiproduct cost structure is economies of scope, which measures the cost savings from product diversity when production is joint-in-inputs. Scope economies allow firms to enjoy cost savings of large quantities while producing smaller amounts of a variety of products. An important source of scope economies is weak cost complementarities. A cost (anti-) complementarity exists between products i and j if increased production of Y_j (raises) lowers the marginal cost of Y_i [2]. Measures of shadow cost complementarities are derived from the relationship between the two $M \times M$ product matrices [19, 22]: $[\delta^2 C^*[W^*, Y(P; Z)]/\delta Y_i \delta Y_j] = [\delta^2 R[P; Z]/\delta P_i \delta P_j]^{-1}$.

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[4] Because $C^* = W^*Z$ is the shadow cost equation and not the cost function, cost does not explicitly include the output vector as an argument. However, it is possible to show that $W^*Z = C(W^*, Y)$.

[5] The shadow cost can also be interpreted as the value of the marginal product of the input bundle [9].

To the extent that cost anticomplementarities (complementarities) coincide with technical product substitution (complementary) possibilities, reorganizing the product mix in favor of these outputs lowers production costs.[6] For example, if the level of one of two substitute products is constrained by a binding quota, the firm will favor production of the unregulated product if the marginal cost of the unregulated product declines due to cost anticomplementarities.

Product-specific economies of scale. Product-specific economies of scale $S_i(Y)$ measure the change in costs as the quantity of Y_i varies with the quantities in Y_{M-i} held constant. $S_i(Y)$ is increasing, decreasing, or constant as $S_i(Y) > / < / = 1$, respectively [2]. When $S_i(Y) > 1$, firms can lower costs by expanding the scale of production for Y_i and may even become specialized in its production. Thus, both scope economies and increasing product-specific economies of scale can affect a firm's mix and volume of products in response to a quota.

The structure of product-specific economies of scale can also affect quota design. Regulators might favor expanding or contracting the scale of production to lower firms' unit costs. Regulators can also be alerted to a natural resource facing depletion or conservation as product lines expand or contract and whether specialized firms producing a single product are likely. An increasing or decreasing value of $S_i(Y)$ could reinforce or inhibit product mix changes fostered by the alignment of cost (anti-) complementarities and technical product (substitution) complementarity possibilities.

The nature of scope and product-specific scale economies can also help determine cross-subsidization among products. If regulators change cross-subsidization, the overall efficiency of firms may be altered, and entry or exit of firms into the industry can occur.[7]

Multiproduct economies of scale. Multiproduct economies of scale, $S_M(Y)$, describe the behavior of costs for proportional changes in all outputs and inputs. $S_M(Y)$ is measured by [9] C^*/R, where R is total revenue, and is decreasing/increasing/or locally constant as $R > / < / = C^*$. Output quotas can alter the overall scale of production by initially affecting outputs' levels and mixes, and over a longer time period in natural resource industries, by affecting the mix and level of resource abundance. Under increasing scale economies, regulations inhibiting firm growth might deter firm and market efficiency.

Marginal costs and cost elasticities. Information on product-specific marginal costs, cost elasticities, and economies of scale can help set marginal-cost pricing and assess the sensitivity of firms' costs and scale efficiency to quota. Marginal shadow cost elasticities, $\delta \ln C^*/\delta \ln Y_i \delta \ln Y_j$, are used here to evaluate the direction and magnitude of weak shadow cost complementarities.

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[6] With joint-in-inputs production, individual supply curves coincide with that product's marginal cost curve only when the latter is evaluated at the optimum output and input bundles [3].

[7] This and sharing of joint costs are important for conflicts between multispecies and single-product sablefish fixed gear.

3.4. *Production Quotas*

The effects of an output quota on the composition of the output bundle and costs of a previously unregulated firm in a dual framework can be assessed by finding the implicit unit rental rate or tariff for the quota [1, 24], and assessing the elasticities with the price change. Because primal and dual constraints are equivalent at the level of formal analysis in a static, full-information, deterministic framework [23], the implicit unit rental rate or tariff, if imposed instead of the quota, yields the same solution [1, 24].

When firms face competitive market prices, the estimated supply equation for the quota-constrained output Y_i at the point of means can be solved for the efficient unit tax τ: $Y_i = f(P_1, \ldots, P_{i-1}, P_i - \tau, P_{i+1}, \ldots, P_M)$, where y_i is the binding quota. With the Generalized Leontief, the unit quota rent can be written for, say, Y_1:

$$\tau = P_1 - \left[\frac{\sum\limits_{j=2,\ldots,M} A_{1j} P_j^{1/2} Z}{y_1 - A_{11} Z - A_1 Z^2} \right]^2 . \tag{3}$$

The term $[\cdot]^2$ represents the virtual price of y_1.[8]

3.5. *Demand Function for Effort*

The impact of a quota upon effort can be evaluated from the demand for effort using the implicit unit tariff. The demand for effort can be derived from its inverse demand function $\delta R[P; Z]/\delta Z = W$, which upon rearrangement gives $Z = g[P, W]$. The elasticity of effort with respect to P_i is

$$\frac{\delta \ln Z}{\delta \ln P_i} = \frac{\left[\sum A_i P_i\right]\left[-A_{ii} - 0.5 \sum\limits_j A_{ij}\left[P_j/P_i\right]^{1/2} - \Omega\right] - \left[W - \sum\sum A_{ij}\left[P_i P_j\right]^{1/2} - \Omega P_i\right] P_i}{2Z\left[\sum A_i P_i\right]^2}, \tag{4}$$

where $\Omega = \Sigma_i \Sigma_k B_{ik} D_k + \Sigma_i \Sigma_l G_{il} E_l$.

4. EMPIRICAL RESULTS

Sablefish output quotas should be consistent with the firm's technology and cost structure to account for regulation-induced changes in the mix and volume of products.[9] This section examines the production technology and shadow cost structure and relates these results to the design of a sablefish trip quota. Costs and elasticities were evaluated at observed sample means and their standard errors were calculated by the delta method.

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[8] Virtual prices are those prices which would induce an unconstrained firm to behave in the same manner as when faced with a given vector of quantity constraints [16, 18].

4.1. Estimation and Hypothesis Testing

We initially estimated each supply equation in (2) by ordinary least squares and found heteroscedasticity of the form discussed by Parks [17], in which the error variance was proportional to the squared input level Z. Each supply equation in (2) was therefore divided by Z. The input-scaled product supply equations were then estimated by Zellner's seemingly unrelated regression technique and iterated to convergence, giving results equivalent to maximum likelihood.[10] The generalized R^2 for the system of equations prior to the heteroscedasticity correction was 0.99, indicating a very good fit for the system.[11]

The likelihood ratio tests results for the structure of technology are reported in Table I. First, however, we tested for overall significance of the quarterly dummy variables, finding them not to be significant as a group. Conditional upon this result, input–output separability and nonjointness-in-inputs for all species as a group were sequentially tested and also rejected. We rejected nonjointness-in-inputs for each individual output except for Dover sole. Dover sole is ubiquitous, and forms a mainstay of the fishery. Dover sole harvesting is unresponsive to product price changes, and firms harvest Dover sole to assure some volume and revenue from production and to satisfy product specifications (demand). We also rejected the null hypotheses of block nonjointness-in-inputs for other flatfish and other rockfish (as a subgroup). Finally, given the maintained hypothesis of non-jointness-in-inputs for Dover sole, the low t-ratios for effort suggested that effort might contribute only at a constant rate to production for thornyheads and other rockfish. The likelihood ratio test result of $A_i = 0$, $i =$ thornyheads and other rockfish, failed to reject constant product-specific returns for these outputs.[12]

Table II reports the estimated final form parameter values of the input-compensated supply equations of Eq. (2), based on the statistical results: (1) no

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[9] Fishery regulation by individual transferable quotas (firm-specific property rights to given catch quantities) can also use our approach, since a firm's responses to market changes must be anticipated to tackle questions such as highgrading.

[10] The form is assumed to be exact rather than an approximation. The errors are from optimization and not approximation, and apply only to the input-compensated supply functions. Some outputs are zero, creating a limited-dependent variable problem which may cause biasedness and non-normality of the residuals [12]. The Box–Cox transformation is not used because it assumes a particular form of non-normality of the residuals before transformation. Virtual prices [11] are not yet computationally feasible with the number of variables in this study. All estimates instead substitute the small value 0.1 when necessary.

[11] The generalized R^2 is computed as $1 - \exp[2(L_0 - L_1)/N]$, where L_0 (L_1) is the sample maximum of log-likelihood when all slope coefficients equal zero (unconstrained) and N is the sample size.

[12] The partial equilibrium product-specific scale elasticity is calculated following Kirkley [6] (where i does not equal j in Σ):

$$E_{iZ}^{\mathrm{PE}} = \frac{Z}{Y_i} = \left[A_{ii} + \Sigma A_{ij}\left[\frac{P_j}{P_i}\right]^{1/2} + 2A_iZ\right].$$

TABLE I

Statistical Tests for Structure of Technology

Test	No. independent restrictions	Chi-square	Reject? (Y/N)
No. quarterly dummy variables	18	21.088	N
Input–output separability	6	36.942	Y
Overall nonjointness	28	5453.870	Y
Nonjointness for:			
Dover sole	5	6.873	N
Thornyheads	5	43.636	Y
Sablefish	5	18.821	Y
Other flatfish	5	30.889	Y
Other rockfish	5	58.871	Y
All others	5	32.444	Y
Block nonjointness of other flatfish and other rockfish	6	92.857	Y
Constant product-specific returns to scale for thorny and other rockfish	2	0.890	N

Note. Likelihood ratio tests with degrees of freedom equal to the number of independent restrictions.

TABLE II

Parameter Estimates of Compensated Supply Functions

Prices and other exog variables	Quantity supplied of					
	Dover sole	Thornyheads	Sablefish	Other flatfish	Other rockfish	All others
Effort	91.631*	22.545*	33.369*	10.181*	58.936*	9.850*
	(10.083)	(1.538)	(5.068)	(1.112)	(6.850)	(1.475)
Effort squared	−0.164*		−0.145*	−0.038*		−0.029*
	(0.077)		(0.030)	(0.009)		(0.011)
Brookings dummy	−31.213*	−11.258*	8.070*	2.218*	28.964*	0.088
	(7.248)	(3.009)	(3.020)	(0.760)	(11.710)	(0.988)
Crescent City dummy	−14.419*	4.800	−1.075	−1.595*	64.125*	−2.123*
	(7.462)	(2.922)	(3.006)	(0.764)	(11.566)	(1.078)
Thornyheads			9.345*	−0.570	−10.841*	−1.405
			(1.735)	(0.414)	(1.527)	(0.623)
Sablefish				−0.340	−2.398	−1.622*
				(0.536)	(1.676)	(0.228)
Other flatfish					−0.026	0.099
					(0.347)	(0.228)
Other rockfish						0.567
						(0.339)

Note. *Statistically significant at 1%. Generalized Leontief functional form. Symmetry and linear homogeneity in prices imposed. Standard errors in parentheses. Apparent heteroscedasticity required estimation of supply per unit of effort. Constant product-specific returns to scale for thornyheads and other rockfish. Nonjointness-in-inputs for Dover sole.

quarterly dummy variables; (2) nonjointness-in-inputs for Dover sole (no price terms for it); and (3), constant product-specific returns to scale for thornyheads and other rockfish (no effort squared terms for these outputs).

4.2. Optimal Fishing Effort

The statistical significance of departure of the service (W) and shadow (W^*) prices of Z may be assessed by a t-test. If the null hypothesis of $W^* = W$ is not rejected, then shadow costs, $C^*[W^*, Y(P; Z)] = W^*Z$, equal full static equilibrium costs, $C[W, Y(W, P)] = C[W, P] = WZ^*(P, W)$, for the profit-maximizing firm. However, the shadow and full static equilibrium multiproduct cost structures (such as scope economies) differ because the long-run expansion effect of $Z^*(P, W)$ is not incorporated into the shadow cost structure; the Appendix provides further results. The result from this t-test also provides equivalent information on the significance of departures between observed (Z) and optimal (Z^*) levels of the quasi-fixed factor, effort [8].

The t-test of the null hypothesis follows Kulatilaka [8]. The shadow price of Z is $\delta R[P; Z]/\delta Z = W^*$, using the observed value of Z and the final form of the technology. The rental price of Z tested against W^* is the 1984 capital services price in units of vessel GRT per trip, derived from vessel acquisition prices in confidential financial statements. The estimated t-statistic is 0.06, where the standard error is calculated by the delta method, and indicates that $W = W^*$, $Z = Z^*(P, W)$, and $C^*[W^*, Y(P; Z)] = C[W, Y(W, P)]$. Because the paper's focus is upon the revenue function and input-compensated supply elasticities, the multiproduct shadow cost structure is evaluated. These results also indicate that the firm's measure of economic capacity utilization equals one, and hence, the firm has no incentives for investment or disinvestment.

4.3. Production Technology

A sablefish quota places the vertical quota supply curve to the left of the unregulated firm's equilibrium level of sablefish catch, intersecting the catch supply curve at the point corresponding to the quota. The supply curve for the quota is for landings rather than catch; i.e., fish can be discarded at sea.

There are two ways in which sablefish catch can match that of quota (landings): (1) a reallocation of the existing (and constant) level of effort during a trip towards other species, so that the firm moves down the sablefish conditional supply curve from the intersection point of the market equilibrium output price to that of the virtual price (where the quota intersects the catch supply) and along the product transformation surface, changing the product mix; (2) over a longer time period, a reduction of effort (not necessarily to the long-run optimum level) in response to quota, shifting the entire sablefish catch supply curve and lowering the level of all products in a normal technology. We consider each of these in turn.

The statistically insignificant own-price sablefish elasticity reported in Table III indicates that the conditional sablefish supply curve for catch is vertical. A quota will not directly reduce the quantity supplied of sablefish by movement down the supply curve to the quota quantity during a fishing trip, since there is not an intersection of the two curves. Hence, the firm will not reallocate effort from sablefish production towards other species. At-sea disposal of sablefish catch

TABLE III

Input-Compensated Price and Scale Elasticities

Prices and effort	Quantity supplied of					
	Dover sole	Thornyheads	Sablefish	Other flatfish	Other rockfish	All others
Thornyheads		0.0006	0.2380*	−0.0676	−0.1712*	−0.0275
		(0.0407)	(0.0442)	(0.0491)	(0.0241)	(0.1219)
Sablefish		0.2279*	−0.1481	−0.0344	−0.0324	−0.2711*
		(0.0356)	(0.1091)	(0.0543)	(0.0226)	(0.1350)
Other flatfish		−0.0150	−0.0095	0.0957*	0.1973*	0.0213
		(0.0109)	(0.0151)	(0.0374)	(0.0060)	(0.0492)
Other rockfish		−0.2110*	−0.0496	−0.0025	−0.0004	0.0901
		(0.0298)	(0.0347)	(0.0334)	(0.0272)	(0.0538)
All others		−0.0025	−0.0308*	0.0088	0.0067	0.1872*
		(0.0112)	(0.0154)	(0.0202)	(0.0040)	(0.0529)
Effort	0.8095	1.0069*	0.2285*	0.0492	1.1167*	0.4586
	(0.4401)	(0.0555)	(0.0203)	(0.3035)	(0.1407)	(0.3837)

Note. *Statistically significant at 1%. Calculated at sample mean for Eureka in the summer. Linearized standard errors in parentheses calculated by the delta method.

above the quota level can be expected, matching sablefish landings and quota and wasting resources.[13]

The sablefish price elasticity of effort of 0.3709, given in Table IV, indicates that effort is quite robust to a binding sablefish quota. This value can be combined with the (inelastic) sablefish-specific scale elasticity of 0.2285, reported in Table II, to indicate the expansion effect upon sablefish supply from a quota and its implicit unit tariff. The product of the two elasticities indicates that a 1% drop in sablefish price reduces sablefish supply by 0.0848% when the firm reduces effort.

A determinate implicit unit tariff or virtual price cannot be found at the point of means for a binding quota of any size because the supply curve for sablefish catch is vertical. However, we can examine the maximum potential decline in effort corresponding to an implicit unit tariff of 99%, when calculated at the sample mean. Hence, the maximum reduction in sablefish supply from the quota-induced reduction in effort, corresponding to a 99% implicit unit tariff, is 232.25 pounds per vessel per trip. Because this maximum possible reduction is substantially less than that required to preclude disposal of sablefish catch for any reasonable size of quota, discards beyond quota can be expected to persist even when the level of effort adjusts in response to quota (but not necessarily to the long-run equilibrium level, in which firms might also exit the industry).

A sablefish quota also affects production through the spillover effects upon the other species. This change in the firm's mix and volume of products, given effort, can impose additional pressure on the biomass of other species. We now examine this issue.

The two most important species harvested with sablefish on the continental slope are Dover sole and thornyheads. Because Dover sole production is unre-

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[13] A reviewer suggested that the sablefish supply curve may be vertical because of targeting and a higher price relative to the other species. In this case, vessels produce the maximum amount in the framework of joint production, and in partial equilibrium respond to quota not by slacking sablefish production, but by discarding smaller, less valuable sablefish ("highgrading").

TABLE IV

Partial Equilibrium Price Elasticity of Effort

Dover sole	Thornyheads	Sablefish	Other flatfish	Other rockfish	All others
0.6359	0	0.3709	0.1757	0	0.0612

Note. Calculated at sample mean for Eureka in summer.

sponsive to changes in prices or output quotas imposed upon other species, a sablefish quota will not have a spillover effect upon it. The statistically significant cross-product supply elasticity between sablefish and thornyheads for a change in either the market or implicit price of sablefish is 0.2279%. Hence, a binding quota on sablefish, or equivalently imposing its implicit unit tariff, will induce a decline in thornyhead production. The production of both sablefish and thornyheads could fall (if the cost structure favors this change) while that of nonjoint Dover sole would remain constant in the regulation-induced trip reorganization of the product mix. The maximum potential decrease in thornyhead supply per trip, corresponding to a 99% implicit unit tariff on sablefish, is 566.29 pounds per vessel when calculated at the sample mean.

The conditional cross-product supply elasticities between sablefish and the other three species groups are negative, inelastic, and statistically significant only for the residual category, all others. Hence, imposition of the implicit unit tariff for sablefish through a binding quota would induce vessels to shift production favoring at least the all others group and perhaps other flatfish and other rockfish (if the cost structure favors this change). Effort is reallocated under quota, not from the constant sablefish production, but from sablefish's complement, thornyheads. As before, a determinate implicit tariff cannot be found at the point of means, but for a 99% implicit unit tariff, the maximum increase in supply per trip is 15.73, 150.56, and 110.54 pounds per vessel for other flatfish, other rockfish, and all others.

4.4. Multiproduct Shadow Cost Structure

Overall economies of scope for joint-in-inputs production of all products except Dover sole are sizable, at 5.17. Cost complementarities predominate in Table V, and many of the cross-product marginal cost relationships are elastic. Incremental costs are negative for sablefish; costs are lowered by adding its harvesting.[14] Product-specific economies of scale are decreasing for other flatfish and all others, and those for thornyheads and other rockfish are constant. The quota should lower or keep constant costs from this source as production levels decline. See Table VI.

The estimate of overall economies of scale is 0.68, indicating decreasing returns. Firms enjoy neither cost nor profit advantages from harvesting more fish in fixed proportions when prices and resource abundance are constant. Ray average costs will rise to the extent that the overall volume of production declines and output proportions remain constant under an output quota.

Quota also affects the firm's implicit marginal valuation of effort, i.e., its shadow cost: $\delta R[P; Z]/\delta Z = W^*(P; Z)$. That is, to the extent that quota induces the

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[14] Resource availability and density preclude the harvesting of other flatfish and all others on a large scale, limiting expanded production opportunities, and giving their high marginal costs.

TABLE V

Marginal Shadow Cost Elasticities

	Marginal shadow cost of				
Output of	Thornyheads	Sablefish	Other flatfish	Other rockfish	All others
Thornyheads	−5.5562	−1.0121	−0.0604	−7.5769	−0.2305
Sablefish	−4.4605	−1.0010	−0.0512	−6.2511	−0.2433
Other flatfish	−1.2355	−0.2375	0.0098	−1.6778	−0.0659
Other rockfish	−6.8320	−1.2790	−0.0773	−7.8912	−0.3149
All others	−0.5061	−0.1212	−0.0071	−0.7668	0.0163

Note. Calculated at sample mean for Eureka in summer using actual marginal costs, i.e., $W^* = W$.

revenue-maximizing firm to reorganize its optimum product bundle, the opportunity cost of revenue foregone will increase, affecting $W^*(P; Z)$ and $C^*[W^*(P; Z), Y(P; Z)]$. The elasticity of W^* with respect to an output price for sablefish, $E_{Wi}^{PE} = \delta \ln W^* / \delta \ln P_i$, is 0.0344%. A 99% implicit unit tax decreases the mean vessel's shadow costs from 26.07 dollars per GRT per trip to 22.66, a decline of 13%. Along with a loss of producer surplus equal to the revenue foregone under quota, firms incur an additional cost equal to the decline in their implicit marginal valuation of effort. Consumer surplus remains constant under the exogenous, competitive output prices.

4.5. *Product Regulation and Flexibility*

The technology and shadow cost structure of these producers indicate only a minimal flexibility to reorganize the mix and volume of outputs other than sablefish and Dover sole. We now examine this result in greater detail.

Scope economies form the principal cost determinant of these firms' economic responses to a trip quota. Scope economies are sizable and extend throughout the set of five joint products and all product-specific scale economies are decreasing or constant. Hence, the alignment pattern of cost (anti-) complementarities with technical product (substitution) complementarity possibilities should play a principal role in determining the firm's reorganization of its product bundle in economic response to quotas.

TABLE VI

Multiproduct Shadow Cost Structure

Product	Incremental costs ($)	Average incremental costs	Product-specific economies of scale	Marginal costs ($/lb)	Cost elasticity
Dover Sole	1,515.58	0.20	0.391	0.46	1.235
Thornyheads	634.56	0.25	0.204	1.15	0.993
Sablefish	−30.50	−0.01	−0.002	4.58	4.377
Other flatfish	30.93	0.22	0.002	127.53	20.306
Other rockfish	1,093.15	0.23	0.389	0.55	0.896
All others	444.84	0.11	0.007	15.35	2.180

Note. Calculated at mean of data set for Eureka in summer. All values in 1984 dollars.

Sablefish's cost complementarity and substitute supply with all others, other rockfish, and other flatfish suggest that product mix changes favoring these products maximize revenues under quota but also raise marginal trip costs. Sablefish's complementarity of marginal cost and product supply with thornyheads suggests that the quota-induced reallocation of (constant) effort from thornyheads to the other joint products lowers both revenues from thornyheads and their marginal cost. Costs should increase for other flatfish and all others due to their decreasing product-specific scale economies.

In sum, the most important economic response by firms to a sablefish trip limit, which considers both the technology and shadow costs, will be only a limited change in the product mix toward all others, possibly other rockfish and other flatfish, and away from thornyheads. Both the cost structure and technology limit the reorganizations in the product line due to the very inelastic cross-product conditional supply elasticities and "misalignment" of the cost structure and technology.

In short, when responding to changing market conditions and output quotas, these firms are not likely to make economic choices that extensively reorganize the volume and mix of their product bundle. An ambitious regulatory plan to induce larger changes in the output bundle than permitted by the firm's inflexible economic capability will leave the industry in its current state of unacceptably high sablefish discards and mortality.

More specifically, a regulatory program consistent with the flexibility of the firm's product decision might be effective only for quotas of such a large size as to be meaningless. When biomass levels face more serious harvesting pressures, a tighter quota is required. But this is overly restrictive for the firm's limited product flexibility and capability to reduce effort, and induces at-sea disposal of sablefish production in excess of the quota.

5. CONCLUDING REMARKS

A command-and-control quota on the individual firm's production of sablefish may be inappropriate. Production has cropped the biomass to a point where increasingly tight production controls are required to keep harvest rates at the requisite level for year-round production under the existing fleet structure. The firm's flexibility of product decision is tightly constrained by its technology and cost structure. As the resource deteriorates and the trip quota progressively tightens, the firm cannot sufficiently adjust its product bundle to preclude increasingly large sablefish disposal. At some quota level, the larger or more productive firms, for which the quota consistently binds, will eventually disinvest or exit the fishery. A trip quota effectively becomes a backdoor limited entry program for vessels which are not necessarily the more inefficient.

An alternative management strategy to more effectively target industry harvesting levels and induce the least efficient firms to exit the industry is required. License limitation, which limits the number of vessels in the fleet, is one possibility, although an effective vessel buy-back program is required to cap production at the appropriate rate when the industry already faces overcapitalization and excessive firm numbers.

A system of individual transferable quotas (ITQs) presents an alternative which is attracting increasing attention among economists. The command-and-control trip quotas examined in this paper would be endowed with property rights to a production flow from the resource stock [20] and be freely transferable between firms. Firms with cost or capacity advantages could purchase quota from other firms. The industry would reorganize by less efficient firms eventually existing the industry, with a lump sum payment, rather than the larger or most productive firms under the current quota system (vessels which may not be less efficient). Given the firm's limited capabilities to alter its product line in response to quota, the major adjustment to quota for some firms—other than disposal—is exit from the sector. But ITQs more efficiently foster this industry restructuring by the more efficient remaining firms compensating the exiting firms.

Yet ITQs in a multispecies fishery can be hampered by the very same inflexible technology limiting the effectiveness of command-and-control quotas. This would defeat the expected benefits of reduced fish mortality and increased technical and arbitrage efficiency. Moreover, because firm exit is a long-run decision, and often involves sunk costs if alternative fisheries or vessel market for exiting vessels are unavailable, the transition period could be longer than expected.[15]

APPENDIX: MULTIPRODUCT COST STRUCTURE

$C^*[W^*(P;Z),Y(P;Z)] = W^*Z = (\delta R[P;Z]/\delta Z)Z = C^*[P;Z]$ is the shadow cost function of the revenue-maximizing firm at the optimal Y for a given Z. In full static equilibrium, $W^* = W$, $Z = Z^*(P,W)$, and $C[W,Y(W,P)] = C[W,P] = WZ^*(P,W)$.

Economies of scope. A twice differentiable multiproduct shadow cost function C^* exhibits weak cost complementarities over the product set I, up to Y, if $\delta^2 C^*(Y'')/\delta Y_i \delta Y_j \leq 0$, i not equal to j, for all Y'' with $0 \leq Y'' \leq Y$, with the inequality holding strictly over a set of nonzero measure.

Measures of shadow cost complementarities are derived from the relationship between the following two $M \times M$ matrices for products: $[\delta^2 C^*[W^*,Y(P;Z)]/\delta Y \delta Y'] = [\delta^2 R[P;Z]/\delta P \delta P']^{-1}$. This result is derived following Sakai [19], so that by marginal-cost pricing: $\delta C^*[W^*(P;Z),Y(P;Z)]/\delta Y' = P'$, where $'$ is the transpose operator. Differentiating with respect to P gives

$$\frac{\delta W^*[P;Z]}{\delta P}\,\frac{\delta^2 C^*[W^*(P;Z),Y(P;Z)]}{\delta W^*\delta Y'} + \frac{\delta Y(P;Z)'}{\delta P}\,\frac{\delta^2 C^*[W^*(P;Z),Y(P;Z)]}{\delta Y\delta Y'} = I,$$

where I is the identity matrix. In terms of the revenue function

$$\frac{\delta^2 R[P;Z]}{\delta P\delta Z'}\,\frac{\delta^2 C^*[W^*(P;Z),Y(P;Z)]}{\delta W^*\delta Y} + \frac{\delta^2 R[P;Z]}{\delta P\delta P'}\,\frac{\delta^2 C^*[W^*(P;Z),Y(P;Z)]}{\delta Y\delta Y'} = I.$$

---

[15] We are grateful to Harry Campbell for this observation.

Note that

$$\left[\frac{\delta^2 C^*}{\delta W^* \delta Y'}\right] = \left[\frac{\delta^2 C^*}{\delta Y \delta W^{*\prime}}\right]' = \left[\frac{\delta(\delta C^*/\delta W^*)}{\delta Y}\right]' = \frac{\delta Z}{\delta Y} = 0,$$

since Z is fixed. Hence, $[\delta^2 C^*[W^*, Y(P; Z)]/\delta Y \delta Y'] = [\delta^2 R[P; Z]/\delta P \delta P']^{-1}$ [17, 20].

The curvature of the shadow cost function can also be inferred directly from the product transformation function $F(Y, Z)$, the latter as defined by Lau [10]. From Lau [10], $[\delta^2 R[P; Z]/\delta P \delta P']^{-1} = [\delta^2 F(Y, Z)]/\delta Y \delta Y']$. Hence, $[\delta^2 C^*[W^*(P; Z), Y(P; Z)]/\delta Y \delta Y'] = [\delta^2 F(Y, Z)]/\delta Y \delta Y']$. Conditions on the Hessian of the transformation function can be directly translated into conditions on the Hessian of the shadow cost function and vice versa.

The relationship between the shadow, $C^*[W^*, Y(P; Z)]$, and full static equilibrium $C[W, Y(P, W)]$ cost functions in output space can be clarified. From Lau [10] and Sakai [19],

$$\frac{\delta^2 C[W, Y(W, P)]}{\delta Y \delta Y'} = \left[\frac{\delta^2 \pi(W, P)}{\delta P \delta P'}\right]^{-1}$$

$$= \left[\frac{\delta^2 R}{\delta P \delta P'} - \frac{\delta^2 R}{\delta P \delta Z'}\left(\frac{\delta^2 R}{\delta Z \delta Z'}\right)^{-1}\frac{\delta^2 R}{\delta Z' \delta P}\right]^{-1},$$

where $\pi(W, P)$ is the full static equilibrium profit function. When W^* does not equal W and at the given Z, $\delta^2 C^*[W, Y(P; Z)]/\delta Y \delta Y' = [\delta^2 R[P; Z]/\delta P \delta P']^{-1}$ as noted above. In full static equilibrium, $W^* = W$ and $Z = Z^*(P, W)$, and the expansion effect is included and all terms are evaluated at W.

The degree of shadow economies of scope at Y relative to product i, $\mathrm{SC}_i(Y)$, is [2] $\mathrm{SC}_i(Y) = [C^*(Y_i) + C^*(Y_{M-i}) - C^*(Y)]/C^*(Y)$, where i and $M - i$ are disjoint product sets. For the partial equilibrium revenue function, $\mathrm{SC}_i(Y)$ is calculated by imposing nonjointness-in-inputs in the revenue function itself (not the conditional supply equations), so that $\delta^2 R[P; Z]/\delta P_i \delta P_j = 0$, and calculating the change in shadow costs.

Product specific economies of scale. $S_i(Y)$ are directly measured by first calculating incremental costs at Y, $\mathrm{IC}_i(Y) = C^*(Y) - C^*(Y_{M-i})$, where Y_{M-i} is a vector with zero components for product i [2]. Incremental (shadow) costs $\mathrm{IC}_i(Y)$ represent the additional total shadow costs incurred by a firm to produce a given level of output i as compared with not producing it at all. Average incremental shadow costs at Y are $\mathrm{AIC}_i(Y) = \mathrm{IC}_i(Y)/Y_i$. $S_i(Y) = \mathrm{AIC}_i(Y)/[\delta C^*(Y)/\delta Y_i]$, where $\delta C^*(Y)/\delta Y_i$ is the marginal shadow cost for product i, MC_i. $S_i(Y)$ are calculated with the revenue (or profit) function by imposing $P_i = 0$ in the revenue function itself (not the conditional supply equations), so that the firm no longer produces Y_i, and then calculating AIC_i.

Multiproduct economies of scale. $S_M(Y)$ is measured by C^*/R, where $C^* = W^*Z$ in partial equilibrium [9], where R is total revenue. As $R >/</=$ total shadow costs, $S_M(Y)$ is decreasing/increasing/or locally constant [2].

Marginal shadow costs and shadow cost elasticities. MC_i at $Y(P; Z)$ with the partial equilibrium revenue function is calculated from the shadow cost equation $C^* = W^*Z$, i.e., $\mathrm{MC}_i = \delta C^*(Y)/\delta Y_i$. The shadow cost elasticity, which indicates the change in total shadow costs for a change in product i, is $\delta \ln C^*/\delta \ln Y_i = (Y_i\ \mathrm{MC}_i)/C^* = [Y_i \delta(W^*Z)/\delta Y_i]/[ZW^*]$.

Partial equilibrium marginal shadow cost elasticities are calculated using the $M \times M$ matrix $[\delta^* R(P; Z]/\delta P_i \delta P_j]^{-1}$, so that the marginal shadow cost elasticity for product i becomes $[\delta^2 R[P; Z]/\delta P_i \delta P_j]^{-1}\ (Y_j/\mathrm{MC}_i)$, $i, j \in M$. Own marginal shadow cost elasticities indicate the slopes of marginal shadow cost curves.

REFERENCES

1. J. E. Anderson, The relative efficiency of quotas: The cheese case, *Amer. Econom. Rev.* **75**, 178–190 (1985).
2. W. Baumol, J. Panzar, and R. Willig, "Contestable Markets and the Theory of Industry Structure," Harcourt Brace Jovanovich, San Diego (1982).
3. B. Beattie and C. Taylor, "The Economics of Production", Wiley, New York (1985).
4. W. E. Diewert, Functional forms for revenue and factor requirements functions, *Internat. Econom. Rev.* **15**, 119–130 (1974).
5. R. Hall, The specification of technology with several kinds of output, *J. Polit. Economy* **81**, 878–892 (1973).
6. J. Kirkley, "The Relationship between Management and the Technology in a Multi-species Fishery: The New England, Georges Bank, Multi-species Fishery", Ph.D. dissertation, University of Maryland (1986).
7. J. Kirkley and I. Strand, Jr., The technology and management of multispecies fisheries, *Appl. Econom.* **20**, 1279–1302 (1988).
8. N. Kulatilka, Are observed technologies at long-run equilibrium? *J. Econometrics* **25**, 253–268 (1985).
9. K. Laitinen, "A Theory of the Multiproduct Firm," North-Holland, Amsterdam (1980).
10. L. Lau, A characterization of the normalized restricted profit function, *J. Econom. Theory* **12**, 131–163 (1976).
11. L. Lee and M. Pitt, Microeconometric demand systems with binding nonnegativity constraints: The dual approach, *Econometrica* **54**, 1237–1242 (1986).
12. G. S. Maddala, "Limited Dependent and Qualitative Variables in Econometrics," Cambridge Univ. Press, Cambridge, U.K. (1984).
13. L. Mahe and H. Guyomard, Supply behavior with production quota and quasi-fixed factors, memo, Institut National de la Recherche Agronomique, Station d'Economie Rurale, France (1989).
14. D. McFadden, Cost, revenue, and profit functions, *in* "Production Economics: A Dual Approach to Theory and Applications" (M. Fuss and D. McFadden, Eds.), Vol. I, North-Holland, Amsterdam (1978).
15. G. Moshini, A model of production with supply management for the Canadian agricultural sector, *Amer. J. Agr. Econom.* **70**, 318–329 (1988).
16. J. Neary and K. Roberts, The theory of household behavior under rationing, *European Econom. Rev.* **13**, 24–42 (1980).
17. R. Parks, Price responsiveness of factor utilization in Swedish manufacturing, *Rev. Econom. Statist.* **53**, 129–139 (1970).
18. E. Rothbarth, The measurement of changes in real income under conditions of rationing, *Rev. Econom. Stud.* **8**, 100–107 (1941).
19. Y. Sakai, Substitution and expansion effects in production theory: The case of joint production, *J. Econom. Theory* **9**, 225–274 (1974).

20. A. Scott, Catch quotas and shares in the fishstock as property rights, *in* "Natural Resource Economics and Policy Applications" (E. Miles *et al*., Eds.), U. of Washington Press, Seattle (1986).
21. D. Squires, Public regulation and the structure of production in multiproduct industries, *Rand J. Econom*. **18**, 232–247 (1987).
22. D. Squires, Production technology, costs, and multiproduct industry structure, *Canad. J. Econom*. **21**, 359–378 (1988).
23. M. Weitzman, Prices vs. quantities, *Rev. Econom. Stud*. **41**, 50–65 (1974).
24. A. D. Woodland, "International Trade and Resource Allocation," North-Holland, Amsterdam (1982).

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Patterns of Gene Flow and Genetic Divergence in the Northeastern Pacific Clinidae (Teleostei: Blennioidei), Based on Allozyme and Morphological Data

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Genetic relationships and distribution patterns among populations, subspecies, and species of northeastern Pacific myxodin clinids were analyzed from allozyme data. The most recent revision recognized six species and 12 subspecies in two genera, *Heterostichus* and *Gibbonsia*. Allozymes from 40 gene loci from all 12 nominal taxa were analyzed to compare heterozygosity levels, Hardy-Weinberg equilibrium conformance, genetic distances, and phylogenetic relationships. Sample sites ranged from Carmel, California, to central Baja California, Mexico, and included areas of sympatry, disjunct distribution, and relative isolation. Offshore island sites included the California Channel, San Benito, and Guadalupe islands; the last with several endemic nominal taxa. In addition, morphological characters putatively defining closely related taxa were reexamined because preliminary data suggested that some taxonomic separations had been made on the basis of sexually dimorphic characters and ecophenotypic variation.

Most intraspecific samples shared close genetic relationship, consistent with little genetic isolation. Disjunct populations of *G. montereyensis* and *G. metzi* from north of Point Conception, California, and in areas of coldwater upwelling off northern Baja California, Mexico, respectively, are very similar. The Channel Island populations are little divergent from those of the mainland, however, the San Benito Islands population is slightly more genetically distinct. Populations of the geographically isolated Guadalupe Island are genetically divergent. Patterns of genetic relationships among populations may be explained by the relatively long larval life of clinids (up to two months), geographic continuity, and major coastal current patterns. Some allelic variation in *G. elegans*, *G. montereyensis*, and *G. metzi* also supports longitudinal clinal trends, which may suggest selection resulting from temperature.

Both allozyme and morphological data failed to separate *G. erythra* from *G. montereyensis*. *Gibbonsia erythra* is a deepwater ecophenotype of *G. montereyensis*; males inhabit deeper water than females, and the supposed distinguishing characters are sexually dimorphic and/or depth related. *Gibbonsia norae* is a semi-isolated population of *G. montereyensis* inhabiting the San Benito and Guadalupe islands, Mexico. A new key to the northeastern Pacific Clinidae is given.

MYXODIN clinids or kelpfishes are among the most common temperate nearshore fishes living in benthic algae along the Pacific coast of North America (Williams, 1954; Stepien, 1986a; Stepien et al., 1988). According to C. Hubbs' (1952) revision, the group comprises six species and 12 subspecies in two genera, *Heterostichus* and *Gibbonsia*. The most abundant species of northeastern Pacific myxodins have two general patterns of distribution: north (*G. metzi* and *G. montereyensis*) and south (*G. elegans* and *H. rostratus*) of Point Conception, California (34.5°N, Fig. 1). A temperature boundary at Point Conception roughly separates the northern, cold temperate Oregonian biogeographic region from the southerly warm temperate Cal-

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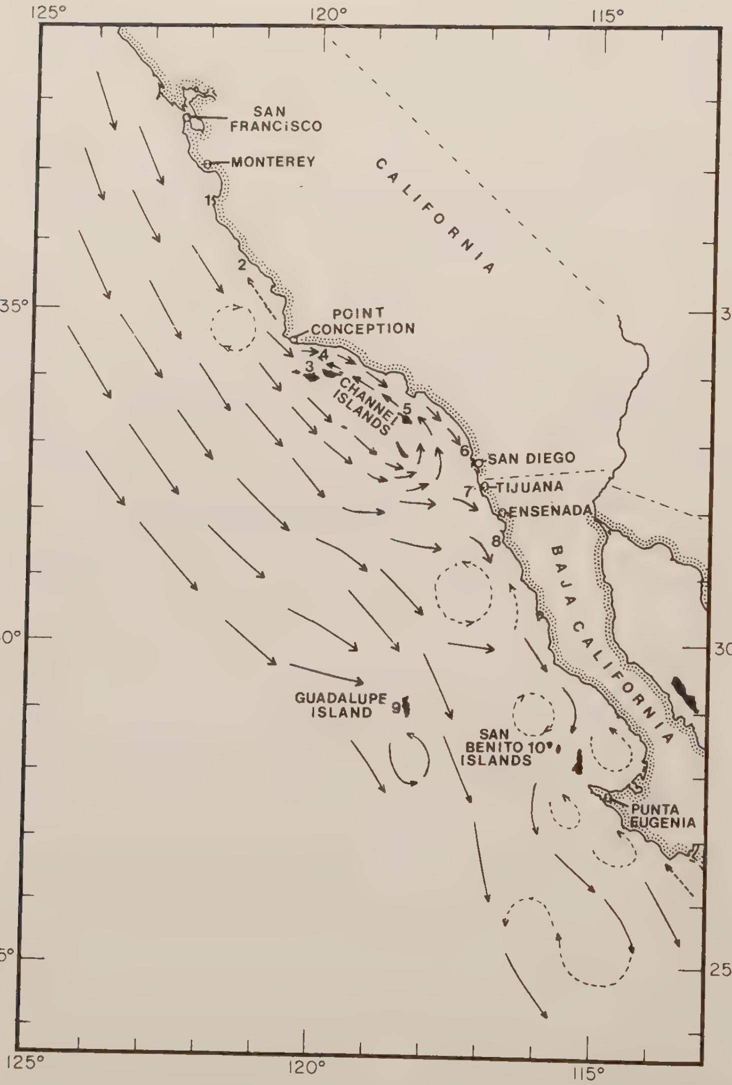
125°
120°
115°
SAN FRANCiSCO
MONTEREY
CALIFORNIA
1
2
35°
POINT CONCEPTION
4
3
CHANNEL ISLANDS
5
6
SAN DIEGO
7
TIJUANA
ENSENADA
8
BAJA CALIFORNIA
30°
GUADALUPE ISLAND
9
SAN BENITO ISLANDS
10
PUNTA EUGENIA
25°

Fig. 1. Location of sample sites, numbered from north to south, as follows: 1 = Carmel, 2 = San Simeon, 3 = Santa Cruz Island, 4 = Santa Barbara, 5 = Santa Catalina Island, 6 = La Jolla (San Diego), 7 = Coronado Islands, 8 = Punta Clara, 9 = Guadalupe Island, 10 = San Benito Islands. Mean current flow patterns in the study area are represented (adapted from Waples and Rosenblatt, 1987 and based on data from Wyllie, 1966; Hickey, 1979; Owen, 1980; and Cowen, 1985). Consistent flow directions are shown with solid arrows; dashed arrows indicate more variable features.

ifornian province (Hedgpeth, 1957; Valentine, 1966; Briggs, 1974; see Table 1 for temperature comparisons). Point Conception is a distributional boundary for many other fishes (C. L. Hubbs, 1960; Horn and Allen, 1978), invertebrates (Garth, 1960; Seapy and Littler, 1980), and algae (Dawson, 1960; Abbott and Hollenberg, 1976; Murray et al., 1980).

However, some of the northern species, including the clinids *G. montereyensis* and *G. metzi*, reappear in pockets of nearshore summer cold water upwelling off Baja California, Mexico, as

Table 1. Mean Seasonal Temperatures (C) Near Some Clinid Collection Sites, Summarized from CALCOFI Data 1950–78 (Lynn et al., 1982).

CALCOFI station	Location	Depth (m)	Seasonal mean				Yearly mean
			Jan	Apr	July	Oct	
80052	Point Conception, California	0	13.66	11.95	12.76	16.07	13.61
	34.5°N, 120°60′W	10	13.64	11.66	12.19	15.62	13.30
		20	13.43	11.18	11.48	14.05	12.54
		30	12.21	10.66	10.82	12.73	11.85
90028	Dana Point, California	0	14.27	15.21	19.15	18.57	16.80
	33°N, 118°W	10	14.05	14.46	16.66	17.87	15.79
		20	13.93	13.23	13.57	15.66	14.10
		30	13.68	12.15	11.96	13.81	12.90
100030	Ensenada, Mexico	0	14.61	16.14	17.51	17.32	16.40
	32°N, 116°30′W	10	14.49	15.99	15.03	16.23	15.44
		20	14.24	15.09	13.33	14.42	14.27
		30	13.84	14.28	12.10	13.40	13.43
110035	Punta Baja, El Rosario, Mexico	0	15.72	14.58	16.93	18.59	16.46
	30°N, 116°W	10	15.68	14.47	16.27	18.41	16.21
		20	15.48	13.92	15.14	17.86	15.60
		30	15.27	13.34	14.06	16.52	14.80
110070	Guadalupe Island, Mexico	0	16.05	16.46	18.75	19.93	17.80
	39°N, 118°45′W	10	15.96	16.38	18.51	19.84	17.67
		20	15.85	16.28	18.17	19.79	17.52
		30	15.79	16.17	17.72	19.66	17.34
120035	San Benito Islands, Mexico	0	16.30	15.68	18.64	20.22	17.71
	28.5°N, 116°W	10	16.29	15.33	18.53	19.79	17.49
		20	16.24	15.08	18.18	19.68	17.30
		30	16.17	14.72	17.72	19.16	16.94
120045	Punta Eugenia, Mexico	0	16.67	15.45	18.40	20.60	17.78
	28°N, 115°20′W	10	16.65	15.31	18.10	20.53	17.65
		20	16.55	14.99	16.66	19.79	17.00
		30	16.44	14.22	15.42	18.13	16.05

well as in deeper waters off some of the offshore islands (C. L. Hubbs, 1952, 1960; C. Hubbs, 1952; Garth, 1960). This disjunct coastal distribution pattern, although presumably widespread (C. L. Hubbs, 1952; Dawson, 1960), has been little studied, and we do not know of other investigations that have focused on population genetics of these organisms. One of the goals of the present study was to examine the degree of genetic isolation and gene flow among clinids having this disjunct distribution pattern.

Stepien et al. (1991) recently completed a year-long survey of fishes at one of the intertidal cold-water upwelling sites off northern Baja California (Punta Clara), where some species characteristic of both marine provinces occur sympatrically. For example, four species of clinids (*H. rostratus, G. elegans, G. metzi,* and *G. montereyensis*) were collected in the same tidepools at the Punta Clara upwelling site, which were analyzed in the present study. No other site examined had such diversity of sympatric clinids.

Waples and Rosenblatt (1987) and Waples (1986, 1987) examined gene flow among populations of eight species of warm temperate fishes having primary distributions south of Point Conception. Fishes from some of their study areas were examined in the present study so comparisons can be made. Comparisons were also made with other studies of population genetics of fishes from some of these areas, including the cottid *Clinocottus analis* (Swank, 1979), the hexagrammid *Oxylebius pictus* (Davis et al., 1981), the sciaenids *Genyonemus lineatus* and *Seriphus politus* (Beckwitt, 1983), the serranid *Paralabrax clathratus* (Beckwitt, 1983), the stichaeid *Anoplarchus purpurescens* (Sassaman et al., 1983), the atherinid *Atherinops affinis* (Crab-

TABLE 2. FORMER AND PRESENT STATUS OF THE NORTHEASTERN PACIFIC MYXODIN CLINIDAE.

Former status (C. Hubbs, 1952) and general distribution	Present status
1. *H. rostratus* Girard, 1854	1. *Heterostichus rostratus*
a. *H. r. rostratus* Girard, 1854 —Baja California to Pt. Conception	a. not recognized
b. *H. r. guadalupensis* C. Hubbs, 1952 —Guadalupe Island endemic	b. not recognized
2. *G. elegans* Cooper, 1864	2. *Gibbonsia elegans*
a. *G. e. elegans* Cooper, 1864 —Baja Calif. to Pt. Conception, intertidal	a. not recognized
b. *G. e. velifera* C. Hubbs, 1952 —Baja Calif. to Pt. Conception, offshore	b. not recognized
c. *G. e. erroli* C. Hubbs, 1952 —Guadalupe Island, endemic	c. not recognized
d. *G. e. rubrior* C. Hubbs, 1952 —Guadalupe Island, endemic	d. not recognized
3. *G. metzi* C. L. Hubbs, 1927	3. *Gibbonsia metzi*
a. *G. m. metzi* C. Hubbs, 1952 —Pt. Conception to Alaska	a. not recognized
b. *G. m. ferventer* C. Hubbs, 1952 —Baja California to Pt. Conception	b. not recognized
4. *G. montereyensis* C. L. Hubbs, 1927	4. *Gibbonsia montereyensis*
a. *G. m. montereyensis* C. L. Hubbs, 1927 —Pt. Conception to Alaska, rough water	a. not recognized
b. *G. m. vulgaris* C. Hubbs, 1952 —Pt. Conception to Alaska, calm water	b. not recognized
5. *G. erythra* C. Hubbs, 1952 —Baja California to Pt. Conception, subtidal	5. Placed in the synonymy of *G. montereyensis*
6. *G. norae* C. Hubbs, 1952 —Guadalupe and San Benito Islands, endemic	6. Placed in the synonymy of *G. montereyensis*

tree, 1986), the blenniid *Hypsoblennius jenkensi* (Present, 1987), and the girellid *Girella nigricans* (Orton, 1989).

Gene products from 40 allozyme loci of all six North American myxodin clinid species and 12 subspecies, as defined by C. Hubbs (1952), were analyzed in the present study. Sample sites ranged along the North American Pacific coast from Soberanes Point, Carmel, California, to central Baja California, Mexico, and included several of the offshore islands, e.g., the Channel, Coronado, San Benito, and Guadalupe islands (see Fig. 1). Sample sites represent both the center of the range of each species and areas of infrequent occurrence and sympatry with related species.

Guadalupe Island, the most isolated site sampled, is 275 km west of the coast of central Baja California, Mexico, and surrounded by deep (>3000 m) water (Fig. 1). Several subspecies and one species of clinid were described by C. Hubbs (1952) as endemic to Guadalupe Island (the endemic species was said to also occur at the San Benito Islands; see Table 2). At one time, Guadalupe Island was believed to have many other endemic fishes (C. L. Hubbs and Rechnitzer, 1958; C. L. Hubbs, 1960). However, more recent studies have shown that some of these have more widespread distributions (Greenfield and Wiley, 1968; Briggs, 1974), and other genetic studies have suggested substantial gene flow between some Guadalupe Island and mainland fish populations (other than clinids; Waples and Rosenblatt, 1987; Waples, 1986, 1987; Orton, 1989). An objective of the present study was to test whether, and to what degree, clinid populations from Guadalupe Island are genetically distinct.

Genetic relationships of all clinid taxa (Table 2) were analyzed in the present study, and some of their morphological characters were also reexamined. C. Hubbs (1952) divided the former *G. montereyensis* into three species, erecting *G. erythra* and *G. norae*. *Gibbonsia erythra* was separated from *G. montereyensis* on the basis of a higher anterior portion of the dorsal fin and squamation extending to the edge of the caudal peduncle (as opposed to a naked area on the peduncle, characteristic of *G. montereyensis*). Individuals identifiable as *G. erythra* are most common in deeper subtidal areas south of Point Conception, California. This complex was a particular focus of the present study because preliminary examination suggested that all *G. erythra* are males. *Gibbonsia norae,* endemic to Guadalupe and the San Benito islands, Mexico, was separated on the basis of having a smaller number of dorsal and anal-fin rays and fewer scale rows above the lateral line (C. Hubbs, 1952).

Many of the meristic characters utilized by C. Hubbs (1952) as discriminators overlap considerably among the 12 clinid taxa. In the present study, allozymes provided a data set that was analyzed separately from morphological data to test patterns of relationships and the delineation of taxa. In addition, life-history and ecological data for *H. rostratus* (Stepien, 1986a, 1986b, 1987) and *G. elegans* (Williams, 1954; Stepien et al., 1988) showed that sexual dimorphism is common in this group and suggested that some subspecies were defined on the basis of sexually dimorphic and depth-related characters. Sexes of North American clinids are depth segregated; adult males are usually found deeper than adult females and juveniles (Williams, 1954; Stepien, 1986a, 1987; Stepien et al., 1988), so that single collections are almost always skewed in sex ratio. The deep-versus-shallow subspecies pairs described by C. Hubbs (1952) were, thus, reexamined for sexually dimorphic and depth-related morphological variation, as well as tested for genetic divergence.

Materials and Methods

Species and locations analyzed.—Allozyme data from all species (*H. rostratus, G. elegans, G. metzi, G. montereyensis, G. erythra,* and *G. norae*) and subspecies of North American myxodins, comprising all 12 taxa recognized by C. Hubbs (1952), were analyzed. Our 10 collection localities and general distribution patterns are given in Figure 1 and Table 2, respectively. Specimens were collected by netting intertidally with use of the anesthetic quinaldine or subtidally by scuba diving and were immediately frozen and stored at −40 C. Voucher specimens of representatives from all sites were deposited in the Scripps Institution of Oceanography (SIO) Marine Vertebrates Collection.

Approximately equal numbers of females and males were analyzed for all populations sampled, excepting *G. erythra* (all males). Sexing was based on examination of whole gonads or gonadal tissue, using a dissection microscope. Gonadal maturities were ranked from 1 to 5, following Stepien (1986a), 1 being immature and 5 being ripe. Separation of individuals of *G. erythra* from *G. montereyensis* fit C. Hubbs' (1952) criterion based on degree of squamation on the caudal peduncle and ratio of the height of the first dorsal spine (SH) to head length (HL).

To investigate sexual dimorphism, scale patterns on the caudal peduncle of *G. montereyensis* and *G. erythra* were ranked from 1 to 5, according to increasing degree of scale coverage. Variation of these scale patterns among males and females was tested with chi-square tests (Sokal and Rohlf, 1981). The SH, HL, standard length (SL), and total length (TL) were measured, following the methods of C. Hubbs (1952), using a dissection microscope, for a series of collections of *G. montereyensis* and *G. erythra* from known depths. In addition, comparisons of measurements of caudal peduncle length (PL) : HL and SL and SH : HL and SL were made for *G. elegans erroli* and *G. elegans rubrior* of known depths from Guadalupe Island. All measurements were taken prior to sexing.

Enzyme electrophoresis.—Separate extracts of eye, liver, and muscle were prepared from each specimen. Tissues were homogenized in a 1:1 volume : volume mixture of tissue and 0.1 M potassium phosphate grinding buffer (pH 7; Waples and Rosenblatt, 1987) and centrifuged at 20,000 *g* for 10 min. The supernatant fraction was then subjected to horizontal starch electrophoresis in 12.5% starch gels (Sigma starch; Sigma Chemical Co., St. Louis, Missouri 63178). The enzymes and tissues surveyed, loci scored, and buffer solutions used are listed in Table 3. Staining methods and recipes were adapted from Selander et al., 1971; Waples, 1986; and Buth and Murphy, 1990. Enzyme nomenclature follows recommendations of the International Union of Biochemistry (1984). Alleles are designated with lowercase letters.

Only 34 loci from the Guadalupe Island population of *H. rostratus* and loci from the Guadalupe Island population of *G. elegans* are included because these samples were previously analyzed by Waples (1986), who contributed tis-

TABLE 3. LIST OF ENZYMES SURVEYED IN ELECTROPHORETIC ANALYSES.

Name (E.C. number)	Locus	Tissue*	Buffer**
Acid phosphatase (3.1.3.2)	Acp-1	L	1
	Acp-A	L	1
Aconitase hydratase (4.2.1.3)	Acoh-A	L	1
Adenylate kinase (2.7.4.3)	Ak-A	M	1, 2
Alcohol dehydrogenase (1.1.1.1)	Adh-A	L	2, 3
	Adh-B	L	2, 3
Aspartate aminotransferase (2.6.1.1)	sAat-B	L	1, 2
	sAat-A	M	1, 2
	mAat-A	L, M	1, 2
Creatine kinase (2.7.3.2)	Ck-B	E	2
	Ck-C	L	1, 2
	Ck-A	M	1, 2
Esterase (3.1.1.–)	Est-1	L, M	4
	Est-2	L, M	4
	Est-3	L, M	4
Fumarate hydratase (4.2.1.2)	Fumh-A	L	1, 2
Glucose–6–phosphate dehydrogenase (1.1.1.49)	G6pdh-1	L	2, 3
	G6pdh-2	L	2, 3
Glucose–6–phosphate isomerase (5.3.1.9)	Gpi-A	E, L, M	2, 4
	Gpi-B	M, E	2, 4
Glutamate dehydrogenase (1.4.1.2)	Gtdh-A	L, M	1
Glyceraldehyde–3–phosphate dehydrogenase (1.2.1.12)	Gapdh-C	E, L	1, 2
	Gapdh-A	M	1, 2
Glycerol–3–phosphate dehydrogenase (1.1.1.8)	G3pdh-B	L, M	1, 2
L-Iditol dehydrogenase (1.1.1.14)	Iddh-A	L	1
Isocitrate dehydrogenase (NADP) (1.1.1.42)	sIdh-A	E, L	1, 2
	mIdh-A	E, M	1, 2
L-Lactate dehydrogenase (1.1.1.27)	Ldh-C	E	1, 2
	Ldh-A	E, M	1, 2
	Ldh-B	E, L	1, 2
Malate dehydrogenase (1.1.1.37)	sMdh-B	M	1, 2
	sMdh-A	L	1, 2
Mannose–6–phosphate isomerase (5.3.1.8)	Mpi-A	L, M	2
Phosphoglucomutase (5.4.2.2)	Pgm-A	L, M	1, 2
Phosphogluconate dehydrogenase (1.1.1.44)	Pgdh-A	M	1
Peptidase (glycyl-l-leucine) (3.4.11.–)	Pep-A	L, M	4
Peptidase (l-leucylglycylglycine) (3.4.11.–)	Pep-B	L, M	4
	Pep-3	L, M	4
Superoxide dismutase (1.15.1.1)	sSod-A	L	3
Xanthine dehydrogenase (1.1.1.204)	Xdh-A	L	1, 3

* Tissues: L = liver, M = muscle, E = eye (retina).

** Buffers: 1 = Tris-citric acid pH 6.9, 2 = Tris-citric acid pH 8.0, 3 = Tris-boric acid EDTA pH 8.6, 4 = Lithium hydroxide (recipes adapted from Selander et al., 1971; Shaklee et al., 1982; Waples, 1986; and Buth and Murphy, 1990).

sue samples, fixed gels, and original scored data to this study. Condition of this frozen material precluded further electrophoretic work and fresh samples from Guadalupe Island could not be obtained. Gene products in these Guadalupe Island samples included all of the polymorphic loci determined in the other populations of *Heterostichus* and *G. elegans.* Loci examined included all listed in Table 3 except Acp-1, Est-1, G6pdh-2, Iddh-A, Mpi-A, and Xdh-A for *H. rostratus* and Aat-A, Acp-1, Ck-C, Est-1, Est-2, Gapdh-C, G6pdh-1, G6pdh-2, and Iddh-A for *G. elegans.* All gels and original data were reexamined; and stains, buffers, and scoring corresponded to those used by Waples (1986).

Data analysis.—BIOSYS–1 vers. 1.7 (Swofford and Selander, 1981, 1989) was used to compute measures of genetic variability (heterozygosity, number of polymorphic loci, and F-statistics; Wright, 1965, 1978), to quantify divergence among the geographic samples (contingency table analyses of heterogeneity among populations), to test conformance with Hardy-Weinberg equilibrium expectations (with Levene's, 1949 correction for small samples), and to calculate Nei's (1972) and modified Rogers' (Rogers, 1972; Wright, 1978) genetic distances between all pairwise combinations of taxa. This program was also used to construct distance Wagner trees (Farris, 1972), using modified Rogers' genetic distances (Wright, 1978).

Allozyme data for *G. elegans* from Bird Rock, California, were compared with data collected by R. Waples (1982 collection unpubl.) using chi-square contingency analyses (Sokal and Rohlf, 1981), to test for temporal variation in allelic frequencies. Collections of *G. elegans, G. metzi, G. montereyensis,* and *H. rostratus* made in 1986–87 and 1987–88 from San Simeon, La Jolla, California, and Punta Clara, Mexico, were also analyzed for temporal variation.

All statistical tests and distance clustering analyses were performed twice in the present study, with the full data set of 40 loci for all populations except Guadalupe Island and again with the data set of 31 loci for all populations of *Heterostichus* and *G. elegans.* Analyses of morphological data (chi-square contingency and regression tests) were performed using SYSTAT (Wilkinson, 1988).

RESULTS

Genotypic data for all polymorphic loci of *H. rostratus, G. elegans, G. metzi, G. montereyensis, G. erythra* and *G. norae* populations are presented in Table 4. Measures of genetic variability are given in Table 5. Modified Rogers' (Wright, 1978) and Nei's genetic distances (1972), calculated between all pairs of taxa are given in Table 6. Mean F_{ST} values and chi-square contingency table comparisons of all populations per species are summarized in Table 7. Data in Table 7 are grouped in analyses with and without Guadalupe Island populations, because these populations were significantly divergent.

Most populations of each species showed close genetic relationship (Tables 5–7). Heterozygosity and percent polymorphism levels for *H. rostratus* are somewhat higher than in species of *Gibbonsia.* All populations conformed to expected Hardy-Weinberg equilibria ($P > 0.70$). There was some deviation (not significant; $P > 0.44$) in the San Benito Islands sample of *G. elegans.* That deviation is the result of a single locus (sSod-A; Tables 4, 5). Contingency table, F_{ST} values, and genetic distances showed no significant temporal variation between samples analyzed by Waples (1986) and the present study. There was also no significant temporal variation between collections made in different years from sample sites at La Jolla (*G. elegans*) and the San Benito Islands (*H. rostratus* and *G. elegans*) (see Materials and Methods; Waples, 1986).

Allozymic differences among all populations of all species, except for those from Guadalupe Island, are minor (Tables 5–8; Figs. 2, 3). There are greater differences in populations from Guadalupe Island (Tables 5–8; Figs. 2, 3), which show closest relationship to San Benito Islands and other southern populations (Table 4; Fig. 2). Genetic variation between nominal subspecies and species (as defined by C. Hubbs, 1952) was tested with contingency chi-square tests (Table 8). No significant differences were found among intraspecific populations other than those from Guadalupe Island.

Relationships among taxa are summarized in Figures 2 and 3, which illustrate results of the distance Wagner procedure (Farris, 1972), based on modified Rogers' genetic distances (Wright, 1978). The tree shown in Figure 2, rooted with the South American myxodin *Myxodes viridis*, has a cophenetic correlation of 0.97. Cophenetic correlations for separate analyses of each individual species group are 0.97 for *H. rostratus,* 0.98 for *G. elegans,* 0.99 for *G. metzi,* and 0.99 for *G. montereyensis.*

All of the preserved specimens examined that fit the characters described by C. Hubbs (1952) for *G. erythra* (high dorsal fin and scales extending to the edge of the caudal peduncle) are males. Of 73 specimens examined that were originally identified as *G. erythra* in the SIO collection (and were large enough to be reliably sexed), 24 did not fit the characters. Of these, 19 were females (with caudal squamation patterns ranging from 1 to 3; see Fig. 4) and five were males (with caudal squamation patterns ranked 3). Eighty-six percent (85 of 99) of identifiable adult male *G. montereyensis* fit the characters of *G. erythra.* The remaining 14 specimens had intermediate patterns of squamation ranked 3 (n = 10) and 2 (n = 4; Table 9).

Specimens of *G. montereyensis* from several locations had scale patterns on the caudal peduncle ranging from the naked area on the pedun-

TABLE 4. GENOTYPIC DISTRIBUTIONS OF POLYMORPHIC LOCI FOR CLINID POPULATIONS.

Species and population	Polymorphic loci and number of each genotype												
	sAat-B	*sAcoh-A*	*Acp-A*	*Adh-A*	*Gpi-A*	*sIdh-A*	*Ldh-A*	*Ldh-B*	*Pep-A*	*Pgdh-A*			
H. rostratus													
1. Santa Catalina Island	aa:09 ab:01	aa:01 ab:05 bb:02	bb:08 ab:01	bb:05 ab:04	bb:07 ab:03	bb:07 ab:03	bb:06 ab:03	aa:07 ab:03	cc:09 ac:01	bb:07 ab:01			
2. San Diego	aa:29 ab:01 ac:01	aa:05 ab:15 bb:10	bb:15 ab:05 bc:01	aa:02 ab:12 bb:16	bb:26 ab:09	bb:20 ab:06	aa:02 ab:11 bb:17	aa:15 ab:09 bb:01	cc:26 ac:04	bb:25 ab:05			
3. Punta Clara	aa:06	ab:05 bb:01	bb:04 ab:02	ab:03 bb:03	bb:05 ab:01	bb:05 ab:01	bb:04 ab:02	bb:04 ab:02	cc:06	bb:05 ab:01			
4. San Benito Islands	aa:08 ab:01	aa:01 ab:04 bb:02	bb:09	ab:03 bb:07	bb:08 ab:01	bb:09 ab:01	bb:10	aa:08 ab:02	cc:08 ac:02	bb:09 ab:01			
5. Guadalupe Island*	aa:06	bb:05 ab:01	bb:05	bb:05	bb:05	bb:02	bb:04	aa:06	cc:05 ac:01	bb:05			
	sAat-B	*sAcoh-A*	*Acp-A*	*Adh-A*	*Est-3*	*Fumh-A*	*G3pdh-B*	*Gpi-A*	*Gpi-B*	*sMdh-B*	*Pep-A*	*Pgdh-A*	*Sod-A*
G. elegans													
1. San Simeon	aa:03	aa:03	aa:03	aa:02 ab:01	aa:03	aa:03	aa:02 ab:01	aa:02 ac:01	aa:03	aa:03	aa:03	aa:03	aa:02 ae:01
2. Santa Barbara	aa:09	aa:08	aa:08	aa:08	aa:07	aa:08	aa:07 ab:01	aa:08	aa:07 ac:01	aa:07 ab:01	aa:08	aa:07 ab:01	aa:06 ac:02 ae:01
3. Santa Cruz Island	aa:04	aa:04	aa:03 ad:01	aa:04	aa:04	aa:04	aa:04	aa:03 ac:01	aa:04	aa:04	aa:04	aa:04	aa:03 ac:01
4. Santa Catalina Island	aa:06 ab:01	aa:06 ab:01	aa:05 ad:02	aa:05	aa:05 ab:01 ac:01	aa:07	aa:05	aa:04 ac:01	aa:04	aa:06 ab:01	aa:07	aa:07	aa:06 ac:01
5. La Jolla	aa:56 ab:06	aa:53 ab:04 ac:06	aa:48 ad:05	aa:52 ab:03	aa:47 ab:03 ac:01	aa:47 ab:04	aa:50 ab:06 ac:03 ad:01	aa:45 ac:19 cc:02	aa:35 ac:02	aa:51 ab:10 ac:01	aa:63	aa:55 ab:04	aa:45 ac:06
6. Coronado Islands	aa:04 ab:01	aa:04 ac:01	aa:05	aa:05	aa:05	aa:05	aa:05	aa:04 ab:01	aa:05	aa:04 ab:01	aa:05	aa:05	aa:04 ac:01

TABLE 4. CONTINUED.

Species and population	Polymorphic loci and number of each genotype												
	sAat-B	*sAcoh-A*	*Acp-A*	*Adh-A*	*Est-3*	*Fumh-A*	*G3pdh-B*	*Gpi-A*	*Gpi-B*	*sMdh-B*	*Pep-A*	*Pgdh-A*	*Sod-A*
7. Punta Clara	aa:10	aa:06 ab:01 ac:01	aa:07	aa:08	aa:08 ab:01	aa:08	aa:07	aa:06 ac:02	aa:08 ac:01	aa:08 ab:01	aa:08	aa:07 ab:01	aa:07 ac:01
8. San Benito Island	aa:19 ab:01	aa:03 ac:01	aa:20	aa:10	aa:17 ab:01 ac:01	aa:17 ab:03	aa:19	aa:17 ac:02	aa:14 ac:01	aa:14	aa:16	aa:20	aa:15 ac:02 ec:01
9. Guadalupe Island**	aa:11 ab:01	ac:02 cc:01	aa:13	aa:09	aa:12	aa:13	aa:12 ab:01	aa:12 ad:01	aa:13	aa:13	aa:12 ab:01	aa:13	aa:10
	sAcoh-A	*Acp-A*	*Est-3*	*Fumh-A*	*Gpi-A*	*Gpi-B*	*sMdh-B*	*Pep-B*	*Pgdh-A*	*Pgm-A*	*Sod-A*		
G. metzi													
1. Carmel	aa:09 ab:02	aa:10 ad:01	aa:06	bb:09 ab:02	aa:07 ab:03 ac:01	aa:09	aa:08 ad:01 ab:01	cc:10 ac:01	bb:08 ab:02	bb:10 ab:01	aa:09 ac:01		
2. San Simeon	aa:41 ab:07 af:01	aa:41 ad:03	aa:38 ab:02 ac:01	bb:45 ab:07	aa:35 ab:12 ac:01	aa:44 ac:02	aa:46 ab:05 ad:02	cc:44 ac:04	bb:23 ab:05	bb:50 ab:02	aa:45 ac:02		
3. Punta Clara	aa:15 ab:03 af:03	aa:15 ad:02	aa:11 ab:03 ac:03	bb:16 ab:02	aa:15 ab:05	aa:15 ac:01	aa:07 ab:03	cc:15 bc:01	bb:17 ab:01	bb:15 ab:03	aa:16 ac:02		
	sAcoh-A	*Acp-A*	*Est-3*	*Fumh-A*	*G3pdh-B*	*Gpi-B*	*mIdh-A*	*sMdh-B*	*mMdh-A*	*Pep-3*	*Sod-A*		
G. montereyensis													
1. Carmel	aa:07 ab:02	aa:09 ad:01	aa:07 ab:01	bb:09	aa:09	aa:08 ac:02	bb:10	aa:10	bb:07 ab:02	dd:09 ad:01	aa:09 ac:01		
2. San Simeon	aa:21 ab:08 bb:01	aa:23 ad:02	aa:26 ab:02	bb:22 ab:03	aa:20 ab:01 ac:01	aa:22 ac:07	bb:29 ab:02	aa:28	bb:24 ab:06	dd:25 ad:03	aa:15 ac:04		
3. Santa Barbara	aa:03	aa:02 ad:01	aa:02 ab:01	bb:03	aa:03	aa:02 ac:01	bb:03	aa:03	bb:02 ab:01	dd:03	aa:03		
4. Punta Clara	aa:14 ab:04	aa:11 ad:05	aa:17 ab:01	bb:15 ab:02	aa:16	aa:14 ac:04	bb:17 ab:01	aa:15 ab:03	bb:17 ab:01	ad:01 dd:18	aa:16 ac:02		

Table 4. Continued.

Species and population	Polymorphic loci and number of each genotype										
	sAcoh-A	*Acp-A*	*Est-3*	*Fumh-A*	*G3pdh-B*	*Gpi-B*	*mIdh-A*	*sMdh-B*	*mMdh-A*	*Pep-3*	*Sod-A*
*G. erythra****											
1. San Simeon	aa:06 ab:02	aa:07 ad:01	aa:07	bb:07	aa:07	aa:06 ac:02	bb:08	aa:08	bb:06 ab:01	dd:07 ad:01	aa:07 ac:01
2. Coronado Islands	aa:03 ab:01	aa:02 ad:02	aa:04	bb:03 ab:01	aa:04	aa:03 ac:01	bb:04	aa:03 ab:01	bb:04	dd:04	aa:04
*G. norae****											
1. Guadalupe Island	aa:07 ab:02	ad:03 dd:07	aa:10	bb:07 ab:02	aa:10 ac:01 ad:01	aa:02 ac:05 cc:03	bb:07	aa:09 ab:02	bb:12	dd:12	aa:08 ac:01

* = Allozyme data collected from 34 loci.

** = Allozyme data collected from 31 loci.

*** = Placed in the synonymy of *Gibbonsia montereyensis*.

cle characteristic of the species as described by C. Hubbs (1952) to squamation extending to the edge of the peduncle, characteristic of *G. erythra* (Fig. 4). In reexamining the scale patterns of 217 *G. montereyensis,* we found that significantly more males than females had a completely scaled caudal peduncle (Table 9). There were no significant differences between ratios of SH : HL ($\chi^2 = 2.11$, df = 1, $P = 0.15$) and SH : SL ($\chi^2 = 1.91$, df = 1, $P = 0.17$) for males (n = 102) versus females (n = 109). However, there were significant increases in these ratios with increasing depth (Table 10). There were no significant differences, however, between males from the 10 to 20 m and the 21 to 45 m classes. There was a significant difference between depth distributions of females and males (Table 11). Females dominated intertidal collections, decreasing in overall percentage with increasing depth, and males were most common subtidally, increasing in overall numbers with depth. Genetic distances based on allozyme data among samples identified from morphology as *G. erythra* and *G. montereyensis* are shown in Figure 3, further demonstrating that *G. erythra* cannot be separated genetically from *G. montereyensis.* Clustering reflects geographic, rather than morphotypic, relationships.

Reexamination of the characters distinguishing the Guadalupe Island endemic subspecies *G. elegans erroli* and *G. elegans rubrior* (purportedly differences in SH : HL and PL : HL ratios; C. Hubbs, 1952), from 103 specimens (38 females and 65 males) of known collection depths yielded similar results. Ratios of SH : HL and SH : SL were significantly greater in males than in females ($\chi^2 = 4.94$, df = 1, $P = 0.026$ and $\chi^2 = 5.92$, df = 1, $P = 0.015$, respectively). There was also a significant increase in SH : SL ratio with depth class for females ($\chi^2 = 6.71$, df = 2, $P = 0.035$) and a less significant increase in this ratio with depth for males ($\chi^2 = 2.96$, df = 1, $P = 0.85$). The holotype and three paratypes of *G. elegans rubrior* are all males and all have intermediate SH : HL and SH : SL ratios not significantly different from the mean of males in the population (Mean spine height: SL = 1.44, SD = 0.15, SE = 0.02 for males and SL = 1.35, SD = 0.22, SE = 0.04 for females). There were no significant differences between the sexes in PL : HL or PL : SL ratios ($\chi^2 = 0.40$, df = 1, $P = 0.84$ and $\chi^2 = 0.81$, df = 1, $P = 0.78$, respectively). Measures of PL : HL and PL : SL are directly correlated, and there is no evidence supporting C. Hubbs' (1952) supposition of bi-

TABLE 5. HETEROZYGOSITY AND POLYMORPHISM VALUES FOR POPULATIONS OF NORTHEASTERN PACIFIC CLINIDS.

Species	Population	Mean H per locus	Mean number of alleles per locus	% Polymorphism	
				Direct count	0.95 Criterion
H. rostratus	Catalina Island	0.07 + 0.02	1.25 + 0.07	25.00	25.00
	San Diego	0.07 + 0.02	1.30 + 0.09	25.00	22.50
	Punta Clara	0.07 + 0.03	1.20 + 0.06	20.00	20.00
	San Benito Islands	0.05 + 0.02	1.23 + 0.07	22.50	22.50
	Guadalupe Island*	0.01 + 0.01	1.04 + 0.04	03.57	03.57
G. elegans	San Simeon	0.03 + 0.02	1.10 + 0.05	10.00	10.00
	Santa Barbara	0.02 + 0.01	1.15 + 0.07	12.50	12.50
	Santa Cruz Island	0.02 + 0.01	1.08 + 0.04	07.50	07.50
	Catalina Island	0.03 + 0.01	1.20 + 0.07	17.50	17.50
	San Diego	0.04 + 0.01	1.42 + 0.12	30.00	12.50
	Coronado Islands	0.03 + 0.01	1.12 + 0.05	12.50	12.50
	Punta Clara	0.03 + 0.01	1.20 + 0.07	17.50	17.50
	San Benito Islands	0.02 + 0.01	1.23 + 0.08	17.50	12.50
	Guadalupe Island**	0.04 + 0.02	1.21 + 0.08	21.43	07.14
G. metzi	Carmel	0.04 + 0.01	1.27 + 0.09	22.50	15.00
	San Simeon	0.03 + 0.01	1.38 + 0.11	27.50	12.50
	Punta Clara	0.04 + 0.01	1.32 + 0.09	27.50	20.00
G. montereyensis	Carmel	0.03 + 0.01	1.17 + 0.06	17.50	17.50
	San Simeon	0.04 + 0.01	1.27 + 0.08	25.00	15.00
	Santa Barbara	0.03 + 0.02	1.10 + 0.05	10.00	10.00
	Punta Clara	0.03 + 0.01	1.23 + 0.07	22.50	15.00
*G. erythra****	San Simeon	0.03 + 0.01	1.15 + 0.06	15.00	15.00
	Coronado Islands	0.04 + 0.02	1.12 + 0.05	12.50	12.50
*G. norae****	Guadalupe Island	0.04 + 0.02	1.23 + 0.08	20.00	17.50

* = Allozyme data collected from 34 loci.
** = Allozyme data collected from 31 loci.
*** = Placed in the synonymy of *G. montereyensis.*

modality (the regression equation is $PL = 0.1(SL) - 1.0$; $R^2 = 0.94$, $F = 1664$, $df = 1{,}101$, $P < 0.0001$). Ratios of PL : HL and PL : SL of the holotype and paratypes of *G. elegans rubrior* are not significantly different from the mean of the population (Mean = 0.841, SD = 0.076, SE = 0.007). There was a significant difference between proportions of males versus females at various depths; only females were collected intertidally, and males were more common than females in subtidal waters (Table 11). All females collected subtidally were ripe, having gonadal maturities ranked 4 or 5.

DISCUSSION

Population relationships based on allozyme data.—Mean heterozygosity levels (direct count) for clinid populations (Table 5) approximate previous estimates from allozyme data for other marine fishes (Winans, 1980; Kirpichnikov, 1981; Beckwitt, 1983; Waples and Rosenblatt, 1987), including *G. metzi* (Somero and Soulé, 1974) and species of the labrisomid *Neoclinus* (Fukao and Okazaki, 1987). The Guadalupe Island sample of *Heterostichus* had significantly lower mean heterozygosity and polymorphism levels than the other populations. This may suggest a genetic bottleneck, either by an original colonization by a few individuals (founder effect) or a reduction in population in the relatively recent past (Holgate, 1966; Nei et al., 1975; Chakraborty and Nei, 1977). Alternatively, lower heterozygosity may be a result of selection. Giant kelp (*Macrocystis integrifolia*), which is one of the major habitats of *Heterostichus* (Stepien, 1986a, 1986b, 1987), is not present at Guadalupe Island (C. L. Hubbs, 1960), and the observed difference in genetic variability may be associated with habitat. It is possible that this low heterozygosity and polymorphism may be an artifact of small sample size. In contrast, Guadalupe Island populations of *G. elegans* and *G. montereyensis* have high hetero-

Table 6. Nei's Genetic Distances (1972; Below Diagonal) and Modified Rogers' Genetic Distances (Wright, 1978; Above Diagonal) between All Pairwise Combinations of Populations Sampled of Northeastern Pacific Myxodin Clinids.

Species	Population	Population 1	2	3	4	5	6	7	8	9
H. rostratus	1. Catalina Island	*****	0.025	0.022	0.045	0.109				
	2. San Diego	0.001	*****	0.022	0.057	0.117				
	3. Punta Clara	0.002	0.001	*****	0.049	0.108				
	4. San Benito Island	0.002	0.003	0.003	*****	0.089				
	5. Guadalupe Island*	0.012	0.014	0.012	0.008	*****				
G. elegans	1. San Simeon	*****	0.048	0.049	0.057	0.043	0.057	0.051	0.052	0.140
	2. Santa Barbara	0.002	*****	0.035	0.043	0.037	0.034	0.033	0.033	0.131
	3. Santa Cruz Island	0.002	0.001	*****	0.029	0.031	0.039	0.033	0.034	0.133
	4. Catalina Island	0.003	0.002	0.001	*****	0.030	0.035	0.033	0.037	0.126
	5. San Diego	0.002	0.001	0.001	0.001	*****	0.033	0.022	0.032	0.124
	6. Coronado Island	0.003	0.001	0.002	0.001	0.001	*****	0.031	0.034	0.123
	7. Punta Clara	0.003	0.001	0.001	0.001	0.000	0.001	*****	0.026	0.113
	8. San Benito Island	0.003	0.001	0.001	0.001	0.001	0.001	0.001	*****	0.106
	9. Guadalupe Island**	0.021	0.018	0.018	0.017	0.016	0.016	0.013	0.012	*****
G. metzi	1. Carmel	*****	0.007	0.013						
	2. San Simeon	0.000	*****	0.013						
	3. Punta Clara	0.001	0.001	*****						
G. montereyensis	1. Carmel	*****	0.018	0.029	0.036	0.012	0.048	0.149		
	2. San Simeon	0.000	*****	0.030	0.047	0.018	0.048	0.148		
	3. Santa Barbara	0.001	0.001	*****	0.043	0.030	0.053	0.133		
	4. Punta Clara	0.002	0.002	0.002	*****	0.041	0.023	0.131		
	5. San Simeon***	0.000	0.000	0.001	0.002	*****	0.045	0.146		
	6. Coronado Island***	0.002	0.002	0.003	0.001	0.002	*****	0.117		
	7. Guadalupe Island****	0.023	0.023	0.019	0.018	0.022	0.014	*****		

* = Allozyme data collected from 34 loci.
** = Allozyme data collected from 31 loci.
*** = *G. erythra*
**** = *G. norae*

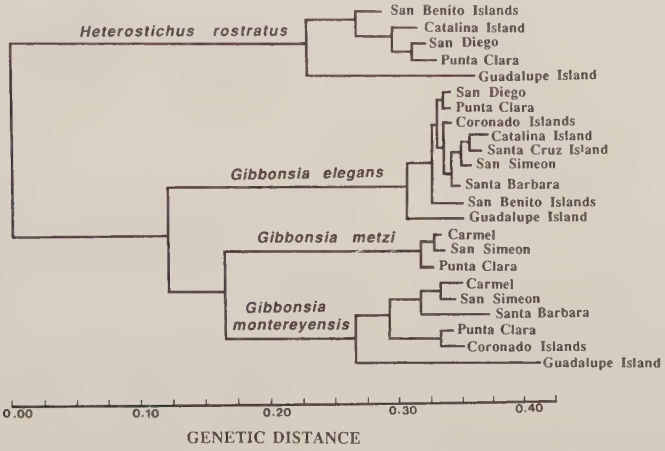
Heterostichus rostratus
San Benito Islands
Catalina Island
San Diego
Punta Clara
Guadalupe Island
Gibbonsia elegans
San Diego
Punta Clara
Coronado Islands
Catalina Island
Santa Cruz Island
San Simeon
Santa Barbara
San Benito Islands
Guadalupe Island
Gibbonsia metzi
Carmel
San Simeon
Punta Clara
Gibbonsia montereyensis
Carmel
San Simeon
Santa Barbara
Punta Clara
Coronado Islands
Guadalupe Island
0.00
0.10
0.20
0.30
0.40
GENETIC DISTANCE

Fig. 2. Distance Wagner tree, illustrating relationships among clinid species and populations and showing relative genetic distances (add lengths of horizontal branches for genetic distances among taxa), rooted to the South American myxodin clinid *Myxodes viridis.*

zygosity and polymorphism levels in comparison to other populations and show some genetic divergence but no suggestion of recent bottlenecks.

Orton (1989), in the girellid *Girella nigricans,* found slightly greater genetic distances between Guadalupe Island and mainland populations than among mainland populations. This was largely a result of the presence of a unique allele at the sSod-A locus in the Guadalupe Island population.

Genetic distances (Table 6) and Wagner clustering relationships (Figs. 2, 3) show little genetic divergence among most clinid populations, excepting that from Guadalupe Island. Waples (1986, 1987) and Waples and Rosenblatt (1987) also found close genetic relationships between populations of several fishes from some of the same areas, including the Channel Islands, San Diego, Punta Eugenia–San Benito Islands, and Guadalupe Island; and Beckwitt (1983) found little variation between populations of three fish species in the southern California bight. However, Present (1987) found a significant allelic frequency difference between populations of the blenny *Hypsoblennius jenkinsi*

TABLE 7. SUMMARY OF F-STATISTICS AND CHI-SQUARE CONTINGENCY TESTS FOR ALLELIC VARIATION AMONG CLINID POPULATIONS, WITH AND WITHOUT GUADALUPE ISLAND SAMPLES.

Species and populations surveyed	Mean F_{ST}	Contingency comparisons Chi-square	df	*P*
H. rostratus				
Without Guadalupe	0.02	29.83	39	>0.855
With Guadalupe	0.07	51.00	52	>0.513
G. elegans				
Without Guadalupe	0.05	116.39	140	>0.927
With Guadalupe	0.13	200.44	52	<0.005*
G. metzi	0.01	29.42	32	>0.598
G. montereyensis				
Without Guadalupe	0.04	39.02	60	>0.984
With Guadalupe	0.15	143.30	84	<0.001*

* = Significant deviation in frequencies of polymorphic alleles between populations based on chi-square contingency tests.

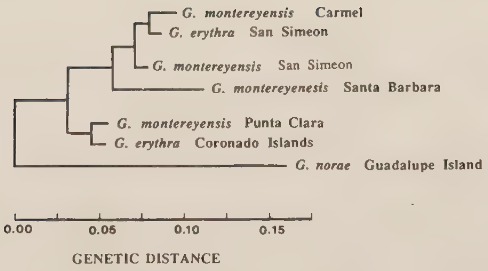
G. montereyensis Carmel
G. erythra San Simeon
G. montereyensis San Simeon
G. montereyenesis Santa Barbara
G. montereyensis Punta Clara
G. erythra Coronado Islands
G. norae Guadalupe Island
0.00
0.05
0.10
0.15
GENETIC DISTANCE

Fig. 3. Distance Wagner tree illustrating relationships among populations of *G. montereyensis, G. norae,* and *G. erythra* and showing relative genetic distances (add lengths of horizontal branches for genetic distances among taxa), rooted to *G. metzi.*

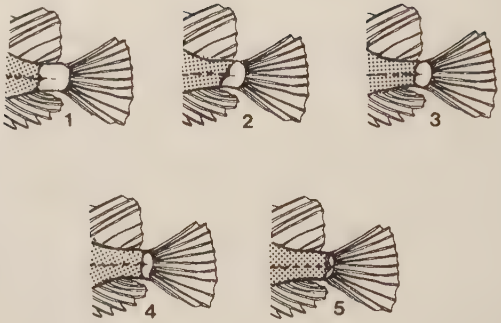

Fig. 4. Drawings of scale patterns on the caudal peduncle of *G. erythra* and *G. montereyensis.* Patterns are ranked from 1 to 5, according to extent of squamation (see Materials and Methods). Scales extend along the body to the point designated on the peduncle. Significant differences between male versus female scale patterns are shown in Table 9.

from two southern California locations, Scripps Pier (La Jolla) and San Diego Bay (separated by approximately 25 km), which was attributed to possible differences in local selection.

Swank (1979) found greater genetic distances separating populations of the cottid *Clinocottus analis* north and south of Point Conception (ranging from 0.006 to 0.044) than were found in the present study. The predominant allele at the Pgm-A locus in the central California populations was abruptly replaced by an alternate allele that predominated in the mainland populations of southern California and Baja California. Davis et al. (1981) found Nei's (1972) genetic distances separating populations of the hexagrammid *Oxylebius pictus* north versus south of Point Conception (ranging from 0.005 to 0.034) that were somewhat greater than those in the present study. This was largely because of the presence of two unique alleles at separate loci; one south and one north of Point Conception. Swank (1979) and Davis et al. (1982) found greater allelic divergences between localities north and south of Point Conception than were found for *G. elegans, G. montereyensis,* and *G. metzi* in the present study.

TABLE 8. CONTINGENCY COMPARISONS OF ALLELE FREQUENCIES AND NEI'S (1972) GENETIC DISTANCES AMONG SUBSPECIES AND CLOSELY RELATED SPECIES.

Taxon A and location	Taxon B and location	Genetic distance D	Chi-square		
			χ^2	df	*P*
H. rostratus guadalupensis Guadalupe Island	*H. rostratus rostratus* San Benito Islands	0.008	11.94	9	>0.217
G. elegans velifera La Jolla	*G. elegans elegans* La Jolla	0.000	16.09	10	>0.097
G. elegans erroli Guadalupe Island	*G. elegans elegans* San Benito Islands	0.012	7.44	17	>0.977
G. metzi ferventer Punta Clara	*G. metzi metzi* San Simeon	0.001	29.42	32	>0.597
G. montereyensis montereyensis Carmel	*G. montereyensis vulgaris* San Simeon	0.000	3.72	11	>0.978
G. erythra San Simeon	*G. montereyensis* San Simeon	0.000	3.28	11	>0.987
G. erythra Coronado Islands	*G. montereyensis* Punta Clara	0.001	2.13	9	>0.989
G. norae Guadalupe Island	*G. montereyensis* Punta Clara	0.018	43.21	12	<0.001

TABLE 9. CONTINGENCY TEST COMPARISONS OF SCALE PATTERN DISTRIBUTIONS (FIG. 3) AMONG MALE AND FEMALE *Gibbonsia montereyensis*.

		Scale pattern					Chi-square contingency test		
Sex	Number	1	2	3	4	5	χ^2	df	*P*
Males	99	00	04	10	36	49			
Females	118	08	57	42	11	00	135.41	4	<0.0005
	217	08	61	52	47	49			

Sassaman et al. (1983) found that Ldh-A in populations of the stichaeid *Anoplarchus purpurescens* ranging from Monterey Bay, California, through Alaska exhibited a longitudinal clinal trend, which was persistent throughout 10 years of sampling. They concluded that stability of geographical differences in allele frequency despite presumptive indications of extensive larval movement between sites suggested that selection, rather than isolation, was the prime force promoting this local differentiation. There is some evidence supporting longitudinal clinal allelic variation in the present study for *G. elegans, G. montereyensis,* and *G. metzi* (Table 6).

Heterostichus rostratus from Santa Catalina Island, San Diego, and Punta Clara have close genetic relationships; Santa Catalina and Punta Clara samples are slightly more genetically distant from each other than either is from the San Diego sample, reflecting geographic proximities. Close genetic relationships and little isolation of Channel Island populations from those of the mainland were also found by Waples (1986, 1987) and Waples and Rosenblatt (1987). However, Swank (1979) found the Catalina Island population of the cottid *Clinocottus analis* to be closer in genetic distance to populations north of Point Conception than to the southern California mainland. Orton (1989) found a significant difference in frequencies of one allele between populations of *Girella nigricans* from Santa Catalina Island and the mainland, although it is possible that this may be an artifact of sample size (n = 8 for the Santa Catalina Island population). Crabtree (1986) also found some genetic differences between populations of the atherinid *Atherinops affinis* from Santa

TABLE 10. CONTINGENCY TEST COMPARISONS OF FIRST DORSAL SPINE HEIGHT : SL AND SH : HL FOR *Gibbonsia montereyensis* FROM VARIOUS DEPTH CLASSES.

	Depth class			
	0–3 m	4–10 m	11–20 m	21–45 m
A. Spine height : head length				
Number sampled	87	78	16	30
Mean	0.53	0.54	0.62	0.57
Standard deviation	0.07	0.08	0.09	0.11
Standard error	0.01	0.01	0.02	0.02
Chi-square	10.43			
Degrees of freedom	3			
Probability	<0.001			
B. Spine height : standard length				
Number sampled	87	78	16	30
Mean	1.15	1.26	1.34	1.31
Standard deviation	0.12	0.19	0.17	0.22
Standard error	0.01	0.02	0.04	0.04
Chi-square	23.03			
Degrees of freedom	3			
Probability	<0.001			

TABLE 11. CONTINGENCY TEST COMPARISONS OF NUMBER OF MALE VERSUS FEMALE *Gibbonsia montereyensis* AND GUADALUPE ISLAND *Gibbonsia elegans* COLLECTED AT VARIOUS DEPTHS.

	Depth class			
	0–3 m	4–10 m	11–20 m	21–45 m
A. *Gibbonsia montereyensis*				
Number of females	75	22	06	06
Number of males	12	56	10	24
Totals	87	78	16	30
Chi-square	72.09			
Degrees of freedom	3			
Probability	<0.0001			
B. *Gibbonsia elegans* (Guadalupe Island population)				
Number of females	07	25	06	—
Number of males	00	42	23	—
Totals	07	67	28	—
Chi-square	15.25			
Degrees of freedom	2			
Probability	<0.001			

Catalina Island and the mainland. The Santa Catalina Island population was most similar to the population sampled from Cedros Island, Baja California, Mexico (which is near San Benito Islands), largely because of lack of a single gene product at a single locus.

The San Benito Islands population of *Heterostichus* is closest in genetic distance to that of Santa Catalina Island, which appears to be similar to Crabtree's (1986) findings for *Atherinops affinis.* Waples and Rosenblatt (1987) also found that San Benito Islands–Punta Eugenia fish populations are more genetically different than those from northern sites and that in most species the closest relationship was to Santa Catalina Island samples, the remainder to La Jolla (San Diego) samples.

Heterostichus from Guadalupe Island are genetically separable from other populations, and their closest relationship is to the San Benito Islands population. For example, both the Guadalupe and San Benito populations uniquely share the losses of the "a" allele at the Acp-A locus and the "a" allele at the Ldh-B locus. These results are similar to relationships between San Benito and Guadalupe Island populations for the labrisomid *Alloclinus holderi* determined by Waples and Rosenblatt (1987).

Individuals of *G. elegans* from San Simeon were collected north of their primary range in Oct. 1986, and were determined (using otolith rings) to be three years old. It is possible that they were recruited from larvae transported north during the 1982 to 1983 El Niño. Our sampling, as well as that by others from this area (in the SIO collection records), indicate that *G. elegans* is relatively rare north of Point Conception.

Our data also are consistent with high levels of gene flow among all populations of *G. elegans* sampled, with genetic relationships largely reflecting geographic proximity (Table 6; Figs. 2, 3). The data also suggest some north to south clinal variation. For example, the "c" allele for the sAcoh-A locus is absent from the four northerly population samples and increases in frequency southward from its appearance in the La Jolla sample. The "b" allele for Est-3 follows a similar pattern, increasing in frequency southward from its appearance in the Santa Catalina Island sample. There are also two cases of apparent allelic absence at geographic extremes. The "b" allele of sMdh-B is absent from the two northernmost populations (San Simeon and Santa Cruz Island) and the two southernmost populations (San Benito and Guadalupe Islands) sampled, and the "b" allele at the sAcoh-A locus is absent from the three northernmost populations (San Simeon, Santa Cruz Island, and Santa Barbara), as well as from the San Benito and Guadalupe islands populations. The "d" allele at the Acp-A locus is present only in the northernmost populations sampled south of Point Conception (Santa Cruz Island, Santa Catalina Island, and La Jolla; Table 4).

Genetic distance data suggest that the San Benito Islands population is little divergent from the other samples, excepting Guadalupe Island. However, the San Benito population is closer in genetic distance to that of Guadalupe Island than are the other populations, as is the case in *Heterostichus.* Guadalupe Island populations of *G. elegans* and *Heterostichus* are greater in genetic distance from other sites but show closer relationship to southern than northern populations.

Populations of *G. metzi* north of Point Conception and in the coldwater upwelling site at Punta Clara (off Baja California) are close in genetic distance (Table 6; Fig. 2). This species has a somewhat disjunct distribution pattern because it is rare off coastal southern California and the offshore islands, reappearing in large numbers in these cold water upwelling areas off Baja California (C. Hubbs, 1952; Stepien et al., 1991). C. Hubbs (1952) considered the populations of *G. metzi* north and south of Point Conception to be subspecifically different. Genetic distances in the present study suggest that this separation is unjustified because even the widely separated areas sampled in the present study show little appreciable genetic divergence. There is some allelic variation between the disjunct populations: notably absence of three alleles in the Punta Clara sample that are present north of Point Conception; the "c" allele at the Gpi-A locus; the "d" allele at the sMdh-B locus; and the "a" allele at the Pep-B locus. The Punta Clara population also has a "b" allele at the Pep-B locus that is absent from samples north of Point Conception. However, this variation in rare alleles, which may reflect clinal differences, and the close genetic distance between them, indicates that they should not be subspecifically separated.

Samples of *G. montereyensis* north of Point Conception and in the Punta Clara upwelling site show also close genetic relationship, consistent with apparent high levels of gene flow (Table 6; Figs. 2, 3). Samples fitting the characters of the nominal *G. erythra* described by C. Hubbs (1952) cannot be separated genetically from *G. montereyensis* (Fig. 3), indicating that *G. erythra* should be placed in the synonymy of *G. montereyensis.* These results are further supported by morphological data, as discussed in the next section. Guadalupe Island samples of the nominal species *G. norae,* erected by C. Hubbs (1952) as endemic to Guadalupe Island and San Benito Islands, show genetic separation comparable to that found in *G. elegans* and *H. rostratus.* These results, together with the paucity of morphological characters delimiting *G. norae* (see next section on morphological variation), suggest that it should be at most a subspecies of *G. montereyensis.*

Genetic distances separating the Guadalupe Island populations of all three clinid species are comparable to those separating other semiisolated fish populations (Vawter et al., 1980; Waples, 1986, 1987; Waples and Rosenblatt, 1987; Grant and Stahl, 1988). These genetic distances (as well as data on morphological variation; see next section) are considerably less than those separating congeneric clinid (Stepien, 1992; see Fig. 2) and labrisomid species (Fukao and Okazaki, 1987; Stepien, 1992). Additionally, Thorpe (1983), utilizing 900 congeneric species comparisons, noted that only some 2% have Nei's (1972) D values below 0.16 and only 0.5% below 0.1.

There is additional support for north-south clinal trends in allelic frequencies in populations of *G. montereyensis* (including *G. erythra* and *G. montereyensis*). The frequency of the "d" allele at the Acp-B locus increases significantly from north to south, with greatest frequency at Guadalupe Island. There are similar southward increases in the frequencies of the "b" allele at the Fum-A locus and the "c" allele at the G3pdh-B locus. There is a unique "d" allele present at the G3pdh-B locus in the Guadalupe Island population.

As in the other clinids, the Guadalupe Island population of *G. montereyensis norae* shows closer genetic relationship to southern populations than to those north of Point Conception. Unfortunately, samples of *G. m. norae* from the San Benito Islands were not obtained in the present study. Waples (1986, 1987) and Waples and Rosenblatt (1987) found that six out of eight species of Guadalupe Island fishes (other than clinids) were closer in genetic relationship to populations from the Channel Islands and La Jolla than to those of the San Benito Islands. Populations of several fishes from San Benito Islands and Punta Eugenia, Baja California (pooled by Waples and Rosenblatt), showed almost as much genetic isolation from northern populations as did those from Guadalupe Island. Relationships of clinid populations from these areas are consistent with those determined by Waples (1987) and Waples and Rosenblatt (1987) for the labrisomid *Alloclinus holderi* and the labrid *Semicossyphus pulcher.*

Mean F_{ST} values for each species (Table 7) indicate little overall genetic variation among populations of *H. rostratus* and *G. metzi* and moderate variation among those of *G. elegans* and *G. montereyensis,* when Guadalupe Island populations are not included (according to genetic divergence levels specified by Wright, 1978, and Hartl and Clark, 1989). With inclusion of Guadalupe Island, *Heterostichus* and *G. elegans* exhibit moderate levels of variation and *G. montereyensis* (including *G. montereyensis norae*) borders on moderate to great genetic variation. Chi-square tests (Tables 7, 8) show no significant differences in overall frequencies of polymorphic alleles among populations of all species and subspecies, when Guadalupe Island populations are excluded. However, there are significant differences in overall allelic frequencies among populations of *G. elegans* and *G. montereyensis* when Guadalupe Island populations are included. The following loci vary significantly: sAcoh-A and Gpi-A in *G. elegans* and Acp-2 and Gpi-B in *G. montereyensis.*

Morphological variation.—C. Hubbs' (1952) analysis of the northeastern Pacific myxodin clinids was based on meristic data, body proportions, and combinations of meristic counts, many of which overlap considerably among groups and show depth-related variation. In examining preserved clinids and samples collected for allozyme data, we found almost all clinid samples to be biased in sex ratio, being either mostly adult males (samples from subtidal waters) or females and juveniles (intertidal samples; see Table 11). This pattern of depth segregation by sex has been previously described for *G. elegans* (Williams, 1954; Stepien et al., 1988; data from the Guadalupe Island population examined in the present study are summarized in Table 11) and *H. rostratus* (Stepien, 1986a, 1987). The same pattern occurs in *G. metzi* and *G. montereyensis* (Table 11), according to material examined in the present study, as well as in the South American myxodin clinid *Myxodes viridis* (Stepien, 1990). Mature female myxodin clinids (e.g., *H. rostratus*) briefly migrate to male territories in deeper water during the spring spawning season to lay eggs in algal nests, which the males guard until hatching (Stepien, 1986a, 1987). If morphological variation between populations and taxa is to be analyzed, depth segregation of the sexes necessitates sexing of all clinid material, as was done in the present study.

Northeastern Pacific myxodin clinids are sexually dimorphic in size; adult females are larger than males at given ages and attain greater lengths (Stepien, 1968a, 1987; Stepien et al., 1988). Such size dimorphism was previously suggested by C. Hubbs (1952) for *G. metzi* and occurs in all species examined in the present study.

In addition, there is sexual dichromatism in *Heterostichus rostratus* (color morphs; Stepien, 1986b, 1987) and *G. elegans* (belly color; Stepien et al., 1988). Deepwater male *G. elegans* (designated as *G. elegans velifera* and *G. elegans rubrior* by C. Hubbs, 1952) and *G. montereyensis* (designated as *G. erythra*) have distinctive red or red-brown color patterns with prominent ocelli on the body above the lateral line (C. Hubbs, 1952; Stepien, unpubl.). Their color matches the red algae among which they live and guard nests. Females and juveniles in shallower areas occur in a variety of red, green, and brown color patterns, which also match their algal habitats (Stepien et al., 1988). Some of these variations in color pattern were considered by C. Hubbs (1952) to characterize various subspecies. Results of the present study suggest that color pattern variation within taxa (red and red-brown colors of deepwater specimens of *G. elegans erythra, G. elegans rubrior,* and *G. erythra*) is correlated with depth and algal habitat and, in some cases, sex.

C. Hubbs (1952) divided *G. metzi* into two subspecies, *G. m. metzi* north, and *G. m. ferventer* south, of Point Conception on the basis of slight differences in lengths of the caudal peduncle and first anal soft ray, stating, "When these two measurements are added and their proportion to the standard length plotted, their standard deviations scarcely overlap." Allozyme data are consistent with the hypothesis of extensive gene flow between these widely separated populations (central California versus Baja California, Mexico; see Fig. 2) and do not substantiate subspecies designation.

Shallow and deepwater populations of *G. elegans* were separated as the subspecies *G. elegans elegans* and *G. elegans velifera,* which differed slightly in relative proportions of SH : HL and body depth : SL, but not in any meristic characters (C. Hubbs, 1952). Williams (1954) examined 777 specimens of *G. elegans* from various depths and found significant differences in sex ratio between shallow and deepwater collections (primarily females in the former and a greater number of males in the latter). Williams' data showed that morphological differences distinguishing *G. elegans elegans* and *G. elegans velifera* were gradual changes resulting from depth-related phenotypic variation. He concluded that differences in sex ratio and morphological intergradiation between the two forms indicated that they represent a single population. In the present study, contingency chi-square tests showed no significant allelic variation between deep water *G. elegans velifera* (all males) and shallow *G. elegans elegans* (both males and females; La Jolla sample sites; see Table 8), further corroborating Williams' conclusions.

C. Hubbs (1952) also described two Guadalupe Island subspecies, *G. elegans erroli* and *G. elegans rubrior,* as differing from each other in the same body proportions purportedly distinguishing *G. elegans velifera* from *G. elegans elegans. Gibbonsia elegans rubrior* was described from four specimens (the holotype and paratypes; which were examined in the present study and found to be males); we were not able to obtain any for allozyme work. Allozyme data were analyzed from six intertidal specimens identified as *G. elegans erroli.* Examination of morphological characters from preserved material demonstrated that proportional differences supposedly distinguishing *G. elegans erroli* from *G. elegans rubrior* are also a result of sexual dimorphism and depth-related variation.

C. Hubbs (1952) found that the Guadalupe Island population of *G. elegans* differed from those of the mainland by having fewer dorsal spines (31 to 33 versus 32 to 35), as well as in some body proportions. The Guadalupe population was regarded as most similar in morphology to that of the San Benito Islands, which have similar temperatures (Table 1). These population relationships are mirrored by results of the present study based on allozyme data (Table 6; Fig. 2). Allozyme data, sex differences in depth distribution, and morphological evidence suggest that subspecies of *G. elegans* need not be recognized.

Guadalupe Island samples of all three species (*Heterostichus, G. elegans,* and *G. montereyensis*) have somewhat reduced meristic counts, notably number of fin rays, and this is probably related to warmer temperatures (Lynn et al., 1982; Table 1). Many other fishes exhibit temperature-related variation in meristics, such as fin ray counts, which are reduced in warmer waters (C. L. Hubbs, 1926; Barlow, 1961). The lower counts are correlated with more rapid development at these temperatures and are, thus, not usually genetic. In all cases except one, the Guadalupe Island meristic counts broadly overlap with those of other populations and are closest to the San Benito Islands and central Baja California populations (C. Hubbs, 1952). A possible exception is the reduced number of scale rows above the lateral line in *G. norae* (samples pooled from San Benito and Guadalupe islands), which does not overlap those of *G. montereyensis* examined by C. Hubbs (1952). However, this lack of overlap may be an artifact of sampling, because C. Hubbs (1952) did not include any samples from the mainland south of Ensenada.

C. Hubbs named two subspecies of *G. montereyensis* from areas of high wave action (*G. m. montereyensis*) and lesser wave action (*G. m. vulgaris*), the latter being more common and widely distributed. These subspecies were distinguished on the basis of overlapping differences in relative height of SH and eye diameter. They were not separated by any meristic characters. Specimens from the Soberanes Point, Carmel site were identified as *G. m. montereyensis,* purportedly found only on the Monterey Peninsula and at Port Buchon (C. Hubbs, 1952). All other populations corresponded to *G. m. vulgaris.* Our examinations of preserved material show that SH is correlated with depth (Table 10), as in *G. elegans* (Williams, 1954). Allozyme data show no genetic differences between these subspecies (Tables 4, 6, 8; Figs. 2, 3), and the proportional differences appear nominal and a result of ecological variation.

Gibbonsia norae, endemic to San Benito and Guadalupe islands, was separated from *G. montereyensis* by C. Hubbs (1952) on the basis of a smaller number of scale rows above the lateral line and fewer dorsal and anal-fin rays. The former character is the only one distinguishing *G. norae,* because the others show extensive overlap. Lower meristic counts in the San Benito and Guadalupe islands populations are common to all three clinid species and may be a result of their more rapid development in warmer water (Barlow, 1961). Lack of morphological characters distinguishing *G. norae* from *G. montereyensis,* absence of fixed allelic differences, and the relatively small genetic distance separating them (which is comparable to those seen in other Guadalupe Island clinids) indicates that species-level separation is unwarranted. We, thus, suggest that *G. norae* be placed in the synonymy of *G. montereyensis.*

Gibbonsia erythra was said to be found primarily in deeper habitats along southern California, the Channel Islands, and northern Baja California, Mexico (C. Hubbs, 1952). The species was separated from *G. montereyensis* on the basis of scales extending to the edge of the caudal peduncle (as opposed to a naked area on the peduncle characteristic of *G. montereyensis*) and a higher SH. In all but one of the records from the SIO and Los Angeles County Museum (LACM) collections in which more than one specimen was collected (n = 6), *G. erythra* were collected sympatrically with *G. montereyensis.* We found that all *G. erythra* (fitting the characters given by C. Hubbs, 1952) are males. Additionally, 86% of male *G. montereyensis* fit the definition of *G. erythra.* We examined caudal peduncle squamation in 217 adult *G. montereyensis* from these collections and the fresh material used in the present study. The amount of squamation on the caudal peduncle in *G. montereyensis* varies extensively, ranging from C. Hubbs' (1952) drawing of the pattern characteristic of *G. erythra* to that of *G. montereyensis.* However, patterns of few individuals fit either of these extremes. Scales usually extend further along the sides of the peduncle and in the center (Fig. 4). Our results show that extent of the naked area on the peduncle is correlated with sex (Table 9), females having a significantly lesser degree of squamation than do males. This difference was apparent in the smallest specimens. Allozyme data in the present study demonstrate that there is no genetic divergence between *G. erythra* and *G. montereyensis* (Tables 4, 6; Fig. 3).

Height of the anterior portion of the dorsal fin in the nominal *G. erythra,* as in the nominal *G. elegans velifera* (Williams, 1954), *G. elegans rubrior,* and *G. montereyensis vulgaris,* is positively correlated with depth and characteristic of deep water male-dominated samples. Results of the present study suggest that *G. erythra* and *G. norae* should be placed in the synonymy of *G. montereyensis* (see Table 2). The following key distinguishes the northeastern Pacific clinid species:

KEY TO THE NORTHEASTERN PACIFIC CLINIDAE

1A. Caudal fin forked; snout sharply pointed; more than 30 anal soft rays; 11 or more dorsal soft rays .... *H. rostratus*

1B. Caudal fin slightly rounded; snout not sharply pointed; fewer than 30 anal soft rays; 10 or fewer dorsal soft rays 2

2A. Dorsal soft rays relatively evenly spaced; 7 to 10 dorsal soft rays; ocelli on the body above the lateral line either small or absent .... *G. metzi*

2B. Posterior dorsal soft rays markedly more widely spaced than anterior rays; 4 to 8 dorsal soft rays; often 2 or more ocelli on the body above the lateral line 3

3A. Scales extending well onto caudal rays in both sexes .... *G. elegans*

3B. No (or very few) scales on caudal fin; females often with a scaleless gap on the caudal peduncle .... *G. montereyensis*

Patterns of gene flow and distribution.—Patterns of genetic relationships among populations of all four clinid species may reflect similarities in their life histories, length of larval phase, dispersal patterns, and/or selective forces. Stepien (1986a) found larvae of *Heterostichus* to be planktonic for approximately two months, and species of *Gibbonsia* appear to share that length of larval life (Stepien, unpubl.). Larval collection data show that clinids are sometimes collected some distance offshore throughout the southern California bight (G. Moser and G. McGowen, pers. comm.; Stepien, unpubl.), and the species may, thus, be capable of long distance dispersal. In addition, adults and juveniles have been found rafting offshore in pieces of drift algae (Stepien, unpubl.). This capacity for dispersal may account for the apparent high levels of genetic uniformity found among clinid populations.

In the present study, disjunct populations of the cooler-water species, *G. metzi* and *G. montereyensis* showed surprisingly little genetic divergence considering the distance between the sites north of Point Conception and at the Punta Clara, Baja California upwelling site. South of Point Conception, these species are found in cold water locations such as the upwelling areas of northern Baja California, as well as subtidally off the mainland and some of the Channel Islands (C. Hubbs, 1952; Stepien et al., 1991). The combination of long planktonic larval life and coastal current patterns (Fig. 1) may also serve to transport them long distances before settlement, maintaining high levels of gene flow.

Patterns of genetic relationships among populations of all species corresponded to geographic proximities. Presumed gene flow patterns also appear related to the major offshore currents (Fig. 1), which probably serve as avenues of larval transport. For example, the Channel Islands are little divergent from mainland populations, as found in other studies of fishes by Waples (1986, 1987) and Waples and Rosenblatt (1987). Similarly, populations of *G. elegans* and *G. montereyensis* from the Coronado Islands off northern Baja California are genetically close to Punta Clara and San Diego populations. Among populations of *G. elegans,* one of the closest genetic relationships is between Santa Catalina and Santa Cruz islands, which are linked by the offshore eddy pattern shown in Figure 1. In contrast to our findings, Haldorson (1980) found significant variation in gene frequencies between Santa Cruz Island and mainland populations of two species of surfperches (Embiotocidae), which may be linked to their viviparity and consequent reduced vagility. Our results suggest that populations from the San Benito Islands are only slightly divergent from mainland populations, which corresponds to their proximity to the nearest mainland and their apparent link with currents passing close to the mainland (Fig. 1).

The three clinid populations from Guadalupe Island (*Heterostichus, G. elegans* and *G. montereyensis norae*) are significantly more genetically isolated from the other populations. Genetic distances distinguishing them are similar but slightly greater in *G. montereyensis,* which may be a result of its being primarily a more northern (cold water) species. Relative genetic isolation of Guadalupe is probably a result of a combination of factors, including its small size and sharp drop-off (limiting shallow water algal areas available for clinid habitats), considerable distance from mainland and other island populations, the surrounding realm of very deep water, and current patterns that only remotely link it with other clinid populations (Fig. 1). These factors may account for genetic drift and/or natural selection resulting in the divergence of these populations. These populations show a very small degree of genetic divergence and, therefore, no clear-cut genetic characteristics to support their recognition as separate species. Although temperature tolerance experiments (Davis, 1977) showed that *G. metzi* has greater tolerance for warm temperatures than does *G. montereyensis, G. metzi* has not been collected at either the San Benito or Guadalupe islands.

Summary.—In conclusion, although the four species of North American clinids, as defined in the present study, display two general patterns of distribution, either primarily in cooler waters (north of Point Conception and in areas of cold water upwelling) or in warmer waters (south of Point Conception), there is considerable sympatry in the southern coastal upwelling areas, as well as off some of the offshore islands. Our results are consistent with high gene flow among all areas sampled (except Guadalupe Island), including the disjunct populations of the former group, which appears to reflect their high capacity for dispersal. The geographic isolation of Guadalupe Island accounts for the genetic divergence of its clinid populations. There is also some evidence supporting north-south clinal geographic variation, which may suggest temperature-related selection.

Material Examined

Specimens used for allozyme analyses and voucher specimen numbers.—Heterostichus rostratus 10 between 5 and 15 m in depth, Santa Catalina Island, California (SIO 90-81); 35 from trawl samples 5 to 10 m deep, Mission Bay, San Diego (SIO 90-80); 6 intertidally, Punta Clara, Baja California, Mexico (SIO 90-82); 10 between 0 and 15 m in depth, San Benito Islands, Baja California, Mexico (SIO 90-83); 6 between 0 and 20 m in depth, Guadalupe Island, Baja California, Mexico (SIO 90-84); *G. elegans elegans* 3 intertidally, San Simeon, California (SIO 90-88); 9 between 0 and 5 m in depth, Santa Barbara, California (SIO 90-87); 4 between 5 and 15 m in depth, Pelican Bay, Santa Cruz Island, California (SIO 90-90); 10 between 5 and 10 m in depth from Cherry Cove, Santa Catalina Island, California (SIO 90-81); 53 intertidally from Bird Rock, La Jolla, California (SIO 90-85); 5 between 5 and 30 m in depth, Middle Coronado Island, northern Baja California, Mexico (SIO 90-89); 10 intertidally, Punta Clara, Baja California, Mexico (SIO 90-82); 20 between 0 and 20 m in depth, San Benito Islands, Baja California, Mexico (SIO 90-83); *G. elegans velifera* 11 from 10 and 15 m depth, Boomer Beach, La Jolla, Calfornia (SIO 90-86); *G. elegans erroli* 13 intertidally, Guadalupe Island, Baja California, Mexico (SIO 90-84); *G. metzi metzi* 11 intertidally, Soberanes Point, Carmel, California (SIO 90-91); 53 intertidally, San Simeon, California (SIO 90-88); *G. metzi ferventer* 21 intertidally, Punta Clara, Baja California, Mexico (SIO 90-82); *G. montereyensis vulgaris* 10 intertidally Soberanes Point, Carmel, California (SIO 90-91); *G. montereyensis montereyensis* 31 intertidally, San Simeon, California (SIO 90-88); 3 between 10–20 m in depth, Santa Barbara, California (SIO 90-87); 19 intertidally, Punta Clara, Baja California, Mexico (SIO 90-82); *G. norae* 12 intertidally, Guadalupe Island, Mexico (SIO 90-84); *G. erythra* 8 in deep tidepools, San Simeon, California (SIO 90-88); 4 between 20 and 35 meters in depth, middle Coronado Island, Baja California, Mexico (SIO 90-89); *Myxodes viridis* (South American myxodin clinid used for tree rooting) 30 intertidally from Montemar, Vina del Mar, Chile (SIO 87-132).

Preserved material examined.—G. montereyensis SIO 73-220, Piedras Blancas Point, San Luis Obispo, California (20); SIO 80-21, Piedras Blancas Point, San Luis Obispo (19); SIO 69-245-61, San Simeon, San Luis Obispo (10); LACM 39975-9, San Simeon (10); SIO 67-151, San Simeon (60); SIO H47-97, Santa Rosa Island (1); SIO H51-244, Santa Cruz Island (2); SIO H51-227, Santa Catalina Island (5); SIO H48-122, Point Loma (1), SIO H51-23, Punta Banda, Baja California, Mexico (23); SIO H49-173, Rio Santo Tomas (5); SIO 61H47-203, Punta Clara (54); SIO 52-158-61A, San Geronimo Island (17); *G. erythra* SIO 51-244, Santa Cruz Island, California (8); SIO 51-240-61A, Santa Cruz Island (1), SIO 51-249, Santa Cruz Island (32); SIO 51-260-61, SIO 51-251, Santa Cruz island (20); LACM 3-9975-9, San Simeon (7); Santa Rosa Island (1); SIO 51-241-61A, Santa Rosa Island (1); SIO 51-241-61B, Santa Rosa Island (1); SIO 54-190-61, San Miguel Island (1); SIO 58-502-61A, La Jolla (1); SIO 61-527-61A, La Jolla (1); SIO H49-151, South Coronado Island, Baja California, Mexico (2); SIO 58-481-61, Coronado Islands (6); SIO 59-305-61C, Punta Banda (1); SIO H52-215, Bahia San Carlos (1); *G. norae* SIO 65-71, Guadalupe Island, Mexico (8); SIO 65-51, Guadalupe Island (1); SIO 57-190, Guadalupe Island (3); SIO 63-178, Guadalupe Island (2); SIO 70-49, Guadalupe Island (5); SIO 58-492, Guadalupe Island (1); SIO 60-15, Guadalupe Island (3); SIO 63-174, Guadalupe Island (2); SIO 71-108, Guadalupe Island (2); SIO H51-124-61A, Guadalupe Island (7); *G. elegans rubrior* CAS SU 16272, holotype, Guadalupe Island (1); CAS SU 16272, paratypes, Guadalupe Island (3); *G. elegans erroli* and *G. elegans rubrior* (mixed) SIO

50-38, Guadalupe Island (25); SIO 54-213, Guadalupe Island (6); SIO 58-453, Guadalupe Island (18); SIO 58-492, Guadalupe Island (20); SIO 58-497, Guadalupe Island (8); SIO 60-14, Guadalupe Island (15); SIO 60-14-16C, Guadalupe Island (2); SIO 63-184-61B, Guadalupe Island (5).

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Literature Cited

Abbott, I. A., and G. J. Hollenberg. 1976. Marine algae of California. Stanford Univ. Press, Stanford, California.

Barlow, G. W. 1961. Causes and significance of morphological variation in fishes. Syst. Zool. 10: 105–117.

Beckwitt, R. 1983. Genetic structure of *Genyonemus lineatus, Seriphus politus* (Sciaenidae) and *Paralabrax clathratus* (Serranidae) in Southern California. Copeia 1983:691–696.

Briggs, J. C. 1974. Marine zoogeography. McGraw-Hill, New York, New York.

Buth, D. G., and R. W. Murphy. 1990. Appendix 1: Enzyme staining formulas, p. 99–126. *In:* Molecular systematics. D. M. Hillis and C. Moritz (eds.). Sinauer Associates, Sunderland, Massachusetts.

Chakraborty, R., and M. Nei. 1977. Bottleneck effects on average heterozygosity and genetic distance with the stepwise mutation model. Evolution 31:347–356.

Cooper, J. G. 1864. On new genera and species of California fishes. Proc. California Acad. Sci., ser. 1. 3:108–114.

Cowen, R. K. 1985. Large scale pattern of recruitment by the labrid, *Semicossyphus pulcher*: causes and implications. J. Mar. Res. 43:719–742.

Crabtree, C. B. 1986. Systematics and taxonomy of the members of the Atherinopsinae (Pisces: Atherinidae). Unpubl. Ph.D. diss., Univ. of California, Los Angeles.

Davis, B. J. 1977. Distribution and temperature adaptation in the teleost fish genus *Gibbonsia.* Marine Biol. 42:315–320.

———, E. E. de Martini, and K. McGee. 1981. Gene flow among populations of a teleost (painted greenling, *Oxylebius pictus*) from Puget Sound to southern California. *Ibid.* 65:17–23.

Dawson, E. Y. 1960. A review of the ecology, distribution, and affinities of the benthic flora. Symposium: the biogeography of Baja California and adjacent seas. Syst. Zool. 9:93–100.

Farris, J. S. 1972. Estimating phylogenetic trees from distance matrices. Am. Nat. 106:645–668.

Fukao, R., and T. Okazaki. 1987. A study on the divergence of Japanese fishes of the genus *Neoclinus.* Japan J. Ichth. 34:309–323.

Garth, J. S. 1960. Distribution and affinities of brachyuran Crustacea. Symposium: the biogeography of Baja California and adjacent seas. Syst. Zool. 9:105–123.

Girard, C. F. 1854. Observations on a collection of fishes made on the Pacific coast of the United States by Lieut. W. P. Trowbridge, U.S.A., for the Museum of the Smithsonian Institution. Proc. Acad. Nat. Sci. Philadelphia 7:142–156.

Grant, W. S., and G. Stahl. 1988. Evolution of Atlantic and Pacific cod: loss of genetic variation and gene expression in Pacific cod. Evolution 42: 138–146.

Greenfield, D. W., and J. W. Wiley. 1968. Geographic variation in the clingfish *Gobiesox eugrammus* Briggs. Trans. San Diego Soc. Nat. Hist. 15: 131–147.

Haldorson, L. 1980. Genetic isolation of Channel Islands fish populations: evidence from two embiotocid species, p. 433–442. *In:* the Channel Islands: proceedings of a multidisciplinary symposium. D. M. Powers (ed.). Santa Barbara Museum Natural History, Santa Barbara, California.

Hartl, D. L., and A. G. Clark. 1989. Principles of population genetics. 2d ed. Sinauer Assoc., Inc., Sunderland, Massachusetts.

Hedgepeth, J. W. 1957. Marine biogeography, p. 459–482. *In:* Treatise on marine ecology and paleoecology. I. Ecology. J. W. Hedgpeth (ed.). Geol. Soc. Amer. Mem. 67. New York, New York.

Hickey, B. M. 1979. The California current system—hypotheses and facts. Prog. Oceanogr. 8:191–279.

Holgate, P. 1966. A mathematical study of the founder principle of evolutionary genetics. J. Appl. Prob. 3:115–128.

Horn, M. H., and L. G. Allen. 1978. A distributional analysis of California coastal marine fishes. J. Biogeogr. 5:23–42.

Hubbs, C. 1952. A contribution to the classification of the Blennioid fishes of the family Clinidae, with a partial revision of the eastern Pacific forms. Stanford Ichth. Bull. 4:41–165.

HUBBS, C. L. 1926. The structural consequences of modifications of the development rate in fishes, considered in reference to certain problems of evolution. Am. Nat. 60:57–81.

———. 1927. Notes on the blennioid fishes of western North America. Paps. Michigan Acad. Sci., Arts. & Letters, Ann Arbor 7:351–394.

———. 1952. Antitropical distribution of fishes and other organisms. Symposium on problems of bipolarity and of pantemperate faunas. Seventh Pacific Sci. Congr. (Pac. Sci. Assoc.). III:1–6.

———. 1960. The marine vertebrates of the outer coast. Baja California Symposium. Syst. Zool. 9:134–147.

———, AND A. B. RECHNITZER. 1958. A new fish, *Chaetodon falcifer*, from Guadalupe Island, Baja California, with notes on related species. Proc. California Acad. Sci. 29:273–313.

INTERNATIONAL UNION OF BIOCHEMISTRY. NOMENCLATURE COMMITTEE. 1984. Enzyme nomenclature, 1984. Academic Press, New York, New York.

KIRPICHNIKOV, V. S. 1981. Genetic bases of fish selection. Springer-Verlag, New York, New York.

LEVENE, H. 1949. On a matching problem arising in genetics. Ann. Math. Stat. 20:91–94.

LYNN, R. J., K. A. BLISS, AND L. E. EBER. 1982. Vertical and horizontal distributions of seasonal mean temperature, salinity, sigma-T, stability, dynamic height, oxygen, and oxygen saturation in the California current, 1950–1978. CALCOFI Atlas No. 30. Marine Life Research program, Scripps Institution of Oceanography, La Jolla, California.

MURRAY, S. N., M. M. LITTLER, AND I. A. ABBOTT. 1980. Biogeography of the California marine algae with emphasis on the southern California islands, p. 325–339. *In:* The Channel Islands: proceedings of a multidisciplinary symposium. D. M. Powers (ed.). Santa Barbara Museum Natural History, Santa Barbara, California.

NEI, M. 1972. Genetic distance between populations. Am. Nat. 106:283–292.

———, T. MARUYAME, AND R. CHAKRABORTY. 1975. The bottleneck effect and genetic variability in populations. Evolution 29:1–10.

ORTON, R. D. 1989. The evolution of dental morphology in the Girellidae (Acanthopterygii: Perciformes), with a systematic revision of the Girellidae. Unpubl. Ph.D. diss., Univ. of California, Los Angeles.

OWEN, R. W. 1980. Eddies of the California current system: physical and ecological characteristics, p. 237–263. *In:* The Channel Islands: proceedings of a multidisciplinary symposium. D. M. Powers (ed.). Santa Barbara Museum Natural History, Santa Barbara, California.

PRESENT, T. M. C. 1987. Genetic differentiation of disjunct Gulf of California and Pacific outer coast populations of *Hypsoblennius jenkinsi.* Copeia 1987: 1010–1024.

ROGERS, J. S. 1972. Measures of genetic similarity and genetic distance. Univ. Texas Publ. 7213:145–153.

SASSAMAN, C., R. M. YOSHIYAMA, AND J. D. S. DARLING. 1983. Temporal stability of lactate dehydrogenase-A clines in the high cockscomb, *Anoplarchus purpurescens.* Evolution 37:472–483.

SEAPY, R. R., AND M. M. LITTLER. 1980. Biogeography of rocky intertidal macro-invertebrates of southern California islands, p. 307-323. *In:* The Channel Islands: proceedings of a multidisciplinary symposium. D. M. Powers (ed.). Santa Barbara Museum Natural History, Santa Barbara, California.

SELANDER, R. K., M. H. SMITH, S. Y. YANG, W. E. JOHNSON, AND J. B. GENTRY. 1971. Biochemical polymorphism and systematics in the genus Peromyscus. I. Variation in the old-field mouse (*Peromyscus polionotus*). Stud. Genet. Univ. Texas Publ. 6:49–90.

SHAKLEE, J. B., C. S. TAMARU, AND R. S. WAPLES. 1982. Speciation and evolution of marine fishes studied by the electrophoretic analysis of proteins. Pac. Sci. 36:141–157.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometery: the principle and practice of statistics in biological research, 2d ed. W. H. Freeman and Co., San Francisco, California.

SOMERO, G. N., AND M. SOULÉ. 1974. Genetic variation in marine fishs as a test of the niche-variation hypothesis. Nature (London) 249:670–672.

STEPIEN, C. A. 1986a. Life history and larval development of the giant kelpfish, *Heterostichus rostratus* Girard. Fish. Bull. 84:809–826.

———. 1986b. Regulation of color morphic patterns in the giant kelpfish, *Heterostichus rostratus* Girard: genetic versus environmental factors. J. Exp. Mar. Biol. Ecol. 100:181–208.

———. 1987. Color pattern and habitat differences between male, female, and juvenile giant kelpfish. Bull. Mar. Sci. 41:45–58.

———. 1990. Population structure, diets, and biogeographic relationships of rocky intertidal fishes in central Chile: high levels of herbivory in a temperate system. *Ibid.* 47:598–612.

———. 1992. Evolution and biogeography of the Clinidae (Teleostei: Blennioidei). Copeia 1992 (in press).

———, M. GLATTKE, AND K. M. FINK. 1988. Regulation and significance of color patterns of the spotted kelpfish, *Gibbonsia elegans* Cooper. Copeia 1988: 7–15.

———, H. PHILLIPS, J. A. ADLER, AND P. J. MANGOLD. 1991. Biogeographic relationships of a rocky intertidal fish assemblage in an area of cold water upwelling off Baja California, Mexico. Pac. Sci. 45: 63–71.

SWANK, S. 1979. Population genetics and evolution of some intertidal fishes of the genus *Clinocottus.* Unpubl. Ph.D. diss., Univ. of Southern California, Los Angeles.

SWOFFORD, D. L., AND R. B. SELANDER. 1981. BIOSYS–1: a FORTRAN program for the comprehensive analysis of electrophoretic data in population genetics and systematics. J. Heredity 72:281–283.

———, AND ———. 1989. BIOSYS-1 vers. 1.7: a computer program for the analysis of allelic variation in population genetics and biochemical systematics. Illinois Natural History Survey, Champaign, Illinois.

THORPE, J. P. 1983. Enzyme variation, genetic distance and evolutionary divergence in relation to levels of taxonomic separation, p. 131–152. *In:* Protein polymorphism: adaptive and taxonomic significance. G. S. Oxford and D. Rollinson (eds.). Academic Press, London, England.

VALENTINE, J. W. 1966. Numerical analysis of marine molluscan ranges on the extratropical northeastern Pacific shelf. Limnol. Oceanogr. 11:198–211.

VAWTER, A. T., R. H. ROSENBLATT, AND G. C. GORMAN. 1980. Genetic divergence among fishes of the Eastern Pacific and the Caribbean: support for the molecular clock. Evolution 34:705–711.

WAPLES, R. S. 1986. A Multispecies approach to the analysis of gene flow in marine shore fishes. Unpubl. Ph.D. diss., Scripps Inst. Oceanogr., Univ. of California, San Diego.

———. 1987. A multispecies approach to the analysis of gene flow in marine shore fishes. Evolution 4: 385–400.

———, AND R. H. ROSENBLATT. 1987. Patterns of larval drift in southern California marine shore fishes inferred from allozyme data. Fish. Bull. 85:1–11.

WILKINSON, L. 1988. SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, Illinois.

WILLIAMS, G. C. 1954. Differential vertical distribution of the sexes in *Gibbonsia elegans* with remarks on two nominal subspecies of this fish. Copeia 1954: 267–273.

WINANS, G. 1980. Geographic variation in the milkfish *Chanos chanos* I. Biochemical evidence. Evolution 34:558–574.

WRIGHT, S. 1965. The interpretation of population structure by F-statistics with special regard to systems of mating. *Ibid.* 19:394–420.

———. 1978. Evolution and the genetics of populations. Vol. 4. Variability within and among natural populations. Univ. of Chicago Press, Chicago, Illinois.

WYLLIE, J. B. 1966. Geostrophic flow of the California current at the surface and at 200 meters. CalCOFI Atlas No. 4. State of California, Marine Research Committee, La Jolla, California.

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Life History and Ecology of Large Jacks in Undisturbed, Shallow, Oceanic Communities*

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Abstract.–The large jack species *Caranx ignobilis* and *Caranx melampygus* were collected from the nearly pristine shallow waters of the atolls, reefs, and shoals of the Northwestern Hawaiian Islands. Both species were aged by counting daily otolith increments and validating frequency of otolith deposition by marking captive fish with tetracycline. Growth for each species was well described by a von Bertalanffy relationship. Measured growth of captive *C. melampygus* was also in agreement. Gravid fish of both species were found only in April–November; peak spawning season for both was about May–August. Reproduction began at ∼350 mm SL (∼2 years old) in *C. melampygus* and at ∼600 mm SL (∼3½ years old) in *C. ignobilis*. Fecundity of female *C. melampygus* varied approximately as the 1.7 power of body weight. Both species were >90% piscivorous, as judged from combined volume and number of prey and incidence of predation. Crustaceans and cephalopods comprised several percent of the diet of *C. ignobilis*; both groups were present but less important in *C. melampygus*. Both jack species ate gastropods in trace amounts. The overall diet of the two species showed moderate overlap: "Pianka's" index of overlap, $A_{yz} = 0.42$. The rate of food consumption for captive *C. melampygus* was used to estimate the respiratory metabolic coefficient, which in turn was used to estimate respiratory demands for all size-classes of both species. The von Bertalanffy model predicted growth energy, and reproductive energy was estimated from values of the gonadosomatic index. These energy terms were combined to calculate the food consumption required to sustain all size-classes appearing in local catch data. This distribution can be represented by a composite individual for each species consuming a little less than 50 kg/year (*C. melampygus*) and about 150 kg/year (*C. ignobilis*). Rough population estimates indicated that at one well-studied atoll, the two species populations combined may eat over 30,000 metric tons of prey per year. These results suggest a quantitatively important trophic role for these top-level carangid predators.

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Fishery Bulletin, U.S. 89:493–513 (1991).

Large jacks (family Carangidae) are widely distributed in tropical and subtropical waters and are highly prized in local fisheries wherever they occur. Where their populations have not been depleted by fishing, these large, active predators are often abundant, and they are probably important in the ecology of nearshore communities. In particular, *Caranx ignobilis* (Forskal) and *C. melampygus* (Cuvier and Valenciennes) are large carnivores that occur commonly throughout much of the tropical Indo-Pacific. These fast, wide-ranging species occupy the entire water column, but their habitats appear to be mostly demersal. They seem to maintain important ties with the demersal fish and benthic fauna of shallow coastal areas, islands, atolls, and isolated shoals.

In Hawaii, these two species are commonly the most abundant of the large, shallow-water, demersal jacks. Large jacks, and these *Caranx* species in particular, have long been important food and market fishes in Hawaii (Cobb 1905, Hamamoto 1928, Țitcomb 1972). Heavy commercial and recreational fishing pressure has developed, especially in the last several decades (Gosline and Brock 1960, Ralston and Polovina 1982, Ralston 1984, Ralston and Kawamoto 1988, Hawaii DLNR 1989), and stocks in the main, inhabited islands are certainly considerably depressed (Shomura 1987).

Despite their widespread occurrence and importance in fisheries, the species biology and ecology of most jacks have been inadequately studied, and little information is available to guide decisions for fishery management. For species such as *C. ignobilis* and *C. melampygus*, which combine large size, high natural abundance, and aggressive feeding habits, the predatory effects on the demersal fauna might be expected to be significant. Therefore, study of the species biology and ecology of these jacks is important both for manage-

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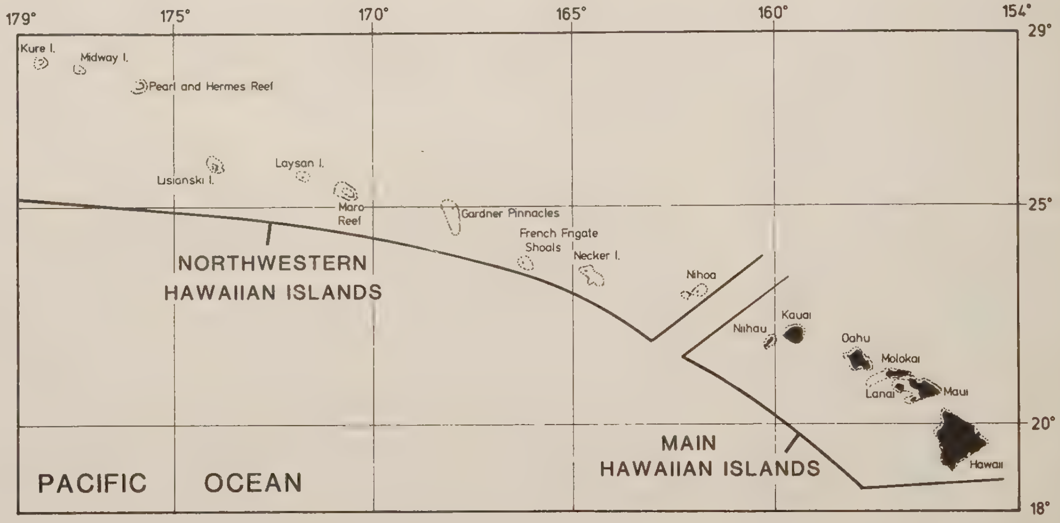

Figure 1
The Hawaiian archipelago. Nearly all specimens analyzed in this study were collected from the Northwestern Hawaiian Islands.

ment of their fisheries and for understanding the ecology of the communities in which they occur.

The uninhabited Northwestern Hawaiian Islands (NWHI) (Fig. 1) offered a particularly appropriate study area because of their size, isolation, and almost pristine biotic communities. Their ecology and natural resources were the subject of a 5-year, multi-agency study (Grigg and Pfund 1980, Grigg and Tanoue 1984), which included major trophic work on shallow-water communities by the Hawaii Cooperative Fishery Research Unit (e.g., DeCrosta et al. 1984, Sorden 1984, Parrish et al. 1985, Norris and Parrish 1988). The present study was done in conjunction with this larger program. Results from these relatively undisturbed carangid populations in the NWHI are also relevant for other populations of large jacks and for management of exploited jack populations.

Materials and methods

Collection information

Specimens of one or both species were collected from French Frigate Shoals (FFS), Maro Reef, Midway Islands, Pearl and Hermes Reef, Lisianski Island, and Necker Island (Fig. 1). Samples were obtained by a wide variety of methods, including handlining, trolling, casting, longlining, and spearing by divers using SCUBA. All jacks came from water less than 30 m deep. In atoll waters, they were taken both inside and outside the barrier reefs. Collections were made irregularly between September 1978 and March 1983, including all months of the year except February (*C. melampygus*) and February and December (*C. ignobilis*). A little over half of all specimens were taken in fall (September–November). Night collections were logistically difficult and largely unproductive. Therefore, there is a daytime bias in the sampling that may have influenced dietary results. The unpreserved fish were weighed whole, and the standard (SL), fork (FL), and total (TL) lengths were measured to the nearest millimeter. Guts of all specimens were injected with formalin in the field and/or frozen promptly. Data were taken on a total of 154 *C. melampygus* and 120 *C. ignobilis*.

Age and growth

For a selected group of specimens covering a wide range of sizes of both species, age was estimated by counting short-period increments of carbonate deposition in otoliths (Radtke 1987). The fish were decapitated along a boundary represented by the edge of the operculum. A sagittal cut was then made through the midline of the head and the cranial cavity exposed. The

Table 1

Relationships determined by regression among standard (SL), fork (FL), and total (TL) lengths in millimeters and whole wet body weight (W) in grams for *Caranx melampygus* and *Caranx ignobilis*.

Caranx melampygus			*Caranx ignobilis*		
Functional relationship	Square of correlation coefficient (r^2)	Sample size (n)	Functional relationship	Square of correlation coefficient (r^2)	Sample size (n)
$W = 2.86 \times 10^{-5} (SL)^{2.974}$	0.99	149	$W = 2.30 \times 10^{-5} (SL)^{2.977}$	0.98	118
$SL = 0.929FL + 1.5$	0.99	141	$SL = 0.924FL + 6.0$	0.99	107
$SL = 0.878TL - 17.4$	0.99	140	$SL = 0.855TL - 17.5$	0.98	107
$TL = 1.052FL + 24.3$	0.99	140	$TL = 1.070FL + 35.7$	0.99	107

sagittae were clearly evident in this dissection. Otoliths were removed from each side of the cranial cavity, cleaned, washed, stored in glycerol, then dried at 60°C for 24 hours, and weighed. Right and left otoliths were segregated.

Whole sagittae were embedded in epoxy casting resin and serially sectioned with a low-speed jewelers' saw. Sections 300 µm thick were attached to scanning electron microscope (SEM) viewing stubs with 5-min epoxy and polished with 0.3 µm alumina paste. The polished sections were etched for 1–20 minutes with 6% ethylene diamine tetraacetate (EDTA) with pH adjusted to 8 with sodium hydroxide. The otolith sections were washed in water, dried, coated with gold, and viewed in an SEM at various magnifications.

A sample of five right sagittae were sectioned in different planes as described by Radtke (1987) to determine that the optimum plane for enumerating increments was the transverse frontal plane. With this technique, we believe that no increments were lost in the chosen plane. Smallest increments were counted with the SEM on sections in this plane of the left sagittae of all specimens used for age determination. Increments were counted from sequential SEM images of the otolith surface, starting at the origin (center) and moving to the otolith margin at the rostrum (anterior). With this methodology, the area read for ageing was consistent for all individuals analyzed. On the assumption that one increment equals one day's growth (Pannella 1971 and 1974), the data were fitted to the von Bertalanffy growth equation (Fabens 1965).

A marking study using tetracycline was undertaken to validate the assumption of daily periodicity of otolith increments. Live carangids were collected from Kaneohe Bay, Hawaii by commercial fishermen using bait nets. Six juvenile *C. melampygus* (197–338 mm SL) and four juvenile *C. ignobilis* (113–225 mm SL) were acclimated for 1 month in a tank of flowing seawater 5.5 m in diameter by 0.6 m deep, exposed to natural sunlight. After 1 month, the fish were measured and given an intraperitoneal injection of 27.5 mg/kg wet body weight of oxytetracycline. To reduce trauma to the fish, they were not weighed at the time of the injections, but their weights were estimated from length-weight relationships derived from wild-caught fish (Table 1). The fish were fed *ad libitum* on a diet of raw herring until recapture, when they were sacrificed. Five *C. melampygus* were sampled after 55 days, the sixth *C. melampygus* and the four *C. ignobilis* after 137 days. Upon recapture, all fish were weighed and standard, fork, and total lengths were measured.

Sagittae from all experimental fish were removed, cleaned, dried, and mounted in clear casting resin. Sections were made both perpendicular and parallel to the rostral axis of the otolith. The sections counted were in a transverse frontal plane, much the same as those prepared for the SEM and as described by Radtke (1987). Sections were polished with 400-grit Carborundum wet-dry sandpaper, mounted on glass slides, and viewed at 300× under a binocular microscope with an ultraviolet light source. The number of increments between the fluorescent mark and the outside edge of the otolith was counted and compared with the number of days that the fish was alive after injection.

Reproduction

Sex ratio, spawning season, and size at first reproduction (SFR) were estimated for both species. Gonads were visually examined and classified as male, female, immature, or unknown. These classifications were based on the size, color, morphology, and texture of the gonadal tissue. Gonads from 70 *C. melampygus* and 10 *C. ignobilis* were removed, wet weighed to the nearest gram, and kept frozen for later, more detailed analysis.

Spawning season was estimated by visual examination of gonads and classification of the mature gonads as either developing or gravid (Kesteven 1960). Months were noted in which there was a significant increase in the number of gravid fish collected relative to the number of mature fish with developing gonads. Spawning season was also estimated by using the gonadosomatic index (GSI):

$$\text{GSI} = (\text{gonad wet weight/whole body wet weight}) \times 100.$$

The GSI for each mature individual was plotted against the date of capture. The spawning season was defined as the period of the year during which a significant proportion of the fish had high GSI values.

To determine the SFR, all fish taken during the spawning season were put into size-classes based on standard length (50 mm SL classes for *C. melampygus* and 100 mm classes for *C. ignobilis*). The number and percent of individuals with gravid gonads in each size-class was determined. As body size increased, at sexual maturity the percent of fish with gravid gonads rose sharply. The lower limit of the size-class in which 50% gravid gonads was reached was taken as the SFR. The SFR was transformed to an age at first reproduction by using the length-age relation from the von Bertalanffy growth equation.

Ovaries from gravid females captured during the peak of the spawning season were used to estimate fecundity, which is defined here as the estimated number of mature ova in the gonad of a spawning female at one time (Everhart and Youngs 1981). Three 2 g aliquots from various parts of each ovary were combined and placed in Gilson's fluid (Simpson 1951). This solution hardens and liberates the eggs and breaks down the ovarian tissue. The egg masses were left in this fluid for 2 weeks, then washed with water and the ovarian tissue removed. Subsamples were obtained by using van Dalsen's (1977) technique as modified slightly by Everson (1984). Each ovary sample was brought up to 500 mL with water and mixed with a magnetic stirrer. When a homogeneous mixture was obtained, three 5 mL aliquots were drawn. All ova more than 0.4 mm in diameter in each 5 mL subsample were counted using a binocular dissecting microscope. A fecundity estimate, F, was calculated from the formula

$$F = ((N_1 + N_2 + N_3)/3) \times (500/5) \times (G/S)$$

where N_1, N_2, N_3 = the number of mature ova in each subsample,

G = total gonad weight,

S = weight of the gonad sample placed in the Gilson's fluid.

Diet

Contents were removed from preserved guts and all prey identified to the lowest taxa possible. The number of individuals and volume of each taxon were noted, as well as the length, weight, and extent of digestion. Many fish in advanced states of digestion were identified by using reference collections of Hawaiian fish scales (Sylvester 1969) and skeletons. Whole prey lengths and volumes were approximated in many cases by comparison of the dimensions of recognizable parts with reference specimens of common Hawaiian reef fishes. The index of relative importance (IRI) was calculated, as defined by Pinkas et al. (1971),

$$\text{IRI} = (\text{numerical \%} + \text{volume \%}) \times \text{frequency \%},$$

where, for each predator species,

numerical % = (number of individuals of one prey category divided by total number of prey individuals found in all the guts) × 100,

volume % = (volume of one prey category divided by total volume of all prey found in the guts) × 100,

frequency % = (number of guts containing prey of one category divided by total number of guts that contained any identifiable prey items) × 100.

A measure of dietary overlap between *C. melampygus* and *C. ignobilis* was provided by the index of overlap, A_{yz} (Pianka 1973). The value of the index varies from 1 when diets are identical with respect to proportional IRI composition to 0 when diets are distinct. We calculated the index using the formula

$$A_{yz} = \left(\sum_i p_{iy}\, p_{iz}\right) \Big/ \left(\sum_i p_{iy}^2 \sum_i p_{iz}^2\right)^{1/2},$$

where p_{iy} and p_{iz} are the proportions of the total IRI represented by the ith prey category for predator species y and predator species z, respectively.

The effect of individual predator size on the diet of *C. melampygus* was assessed by comparing the occurrence of prey items found in the guts of sexually immature and mature fish.

Energy budget and population consumption

Ingestion rates were measured in captivity. A group of six *C. melampygus* and a group of four *C. ignobilis* were held in separate sections of a tank of flowing seawater 5.5 m in diameter and 0.6 m deep. Standard, fork, and total lengths were measured for all fish, and then they were allowed to acclimate to the tank for 1 month while being fed raw herring at least once a day. Uneaten food was removed and the weight consumed was calculated for each feeding. Maximum feeding rates were estimated by feeding *ad libitum* at least three times daily during several intensive feeding periods that ranged between 4 and 10 consecutive days each. The fish used in this experiment were not the same individuals used in the tetracycline marking experiment.

Age-specific rations (rates of food consumption) of the two jack species in the wild and annual consumption by their total populations were estimated by using the measured ration in captivity for specimens of one size, together with results obtained by the preceding procedures for growth, reproductive output, and length-weight relationship. Data for the captive specimens were used in the basic energy budget model for fish (Mann 1965 and 1969, Parrish 1975) to obtain the respiratory metabolic rate, Q,

$$kC = Q + S + G$$

where k = ration assimilation coefficient, representing the fraction of the ingested ration available for utilization in metabolic processes,
C = ration, or rate of food consumption,
Q = rate of respiratory metabolism,
S = rate of production of reproductive material,
G = growth rate.

For the captive fish, ration (C) was measured. Growth (G) was both measured and estimated from the von Bertalanffy model. The value of $k = 0.8$ (Winberg 1956:209, Mann 1967 and 1969) was adopted. Since the fish were prereproductive, the reproductive term (S) was absent. The respiratory metabolic coefficient (α) was estimated from the relationship

$$Q = \alpha W^{\gamma},$$

using the calculated Q, the weight (W) of experimental fish, and $\gamma = 0.8$ as a reasonable approximation for most fishes (Winberg 1956:149, Mann 1965 and 1969, Paloheimo and Dickie 1965 and 1966). This coefficient was then used in the original model to calculate Q for fish of any weight, W. No experimental results were available to estimate α directly for *C. ignobilis*. In view of the other similarities with *C. melampygus* and the high probability of strong metabolic similarities, the value of α for *C. melampygus* was also used for *C. ignobilis*. The corresponding growth rate for any weight was derived from the von Bertalanffy model (computing age corresponding to weight from the model directly and evaluating the first derivative of the model at that weight). For fish larger than the SFR, the maximum observed GSI was used with the body weight to estimate the rate of production of reproductive material (S). With all three terms on the right side of the model computed, ration (C) was readily determined for fish of any size.

The size-frequency distribution of the wild population of each species was estimated by pooling length and weight data for all specimens collected in this study with data compiled by the Hawaii Division of Aquatic Resources and the National Marine Fisheries Service: in total, some 253 specimens of *C. melampygus* and 802 of *C. ignobilis*. Weight-class increments of 200 g were used for *C. melampygus* and 500 g for *C. ignobilis*. The fraction in each size-class was multiplied by the appropriate computed ration, and the results were summed to estimate an individual ration representative of the population as a whole. This ration of the representative individual, multiplied by the population size for any area, provides an estimate of consumption rate by the entire population.

Population sizes for both species were estimated for one of the the major study areas, French Frigate Shoals (FFS), using two methods. First, sightings of the species made during 56 visual underwater transect censuses in a variety of shallow-water habitats were pooled. For a crude population estimate, for such wide-ranging species, the distribution of these censuses over the various habitat types was taken as representative of all the habitats occupied by these fishes. Each sighting was expressed as the number of fish seen per unit area. Estimates of the total submerged area of FFS of less than about 20 m depth (the apparent prime depth range of these species locally) were based on data from Atkinson and Grigg (1984), Agegian (1985), and J.J. Polovina (NMFS Honolulu Lab., Southwest Fish. Sci. Cent., pers. commun.). The product of this area and the population density estimates from the visual census provided rough estimates of the total populations of both jack species at FFS.

A second population estimate was based on the assumption that the density of the almost unexploited jack populations at FFS must be higher than the population density indicated by the highest catches on record for other parts of the archipelago where fishing is significant. Data from the highest catches reported (Cobb 1905) were used directly where species were identified in the catch statistics. Where species were reported pooled in the statistics, they were separated by making the assumption that both species of interest occurred as the same percentage of all shallow-water, demersal, large jacks in 1900—the year in which the data of Cobb (1905) were collected—as in 1981–86 (when catch data were available by species). The catches of the two species in 1900, thus reconstructed, were converted to densities using the summed area (Agegian 1985) within these species' habitat depth range around the main, inhabited Hawaiian islands where the 1900 statistics were obtained. These densities provide a lower limit to estimates of the FFS population densities.

The products of jack population estimates with the respective rations of the representative individual for each species produced estimates for total population consumption (or predation pressure), including all prey consumed. The predation pressure on each prey category was obtained by multiplying these total consumptions by the volume percent (as a decimal fraction) for that prey category.

Table 2

Parameters of the von Bertalanffy growth model for *Caranx melampygus* and *Caranx ignobilis* and summary of data used for the regressions.

	Caranx melampygus	*Caranx ignobilis*
L_∞ (asymptotic SL)	897 mm	1838 mm
W_∞* (asymptotic whole wet weight)	17,313 g	120,139 g
K	0.233/year	0.111/year
t_0	−0.044 year	0.097 year
r^2 [correlation coefficient]^2	0.99	0.99
n (sample size)	14	10
Range of SL used	122–660 mm	106–1180 mm
Range of estimated ages	0.51–5.90 year	0.75–9.27 year

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*Based on standard length-weight relationships from Table 1.

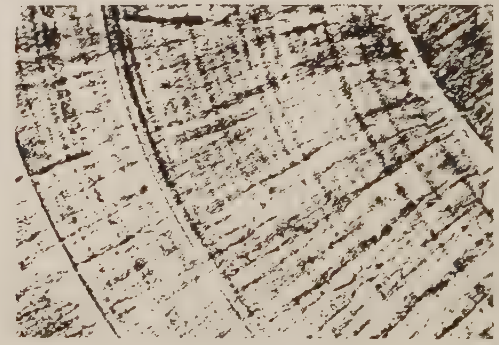

Figure 2

Scanning electron micrograph of a sagitta from *Caranx melampygus*.

Results

Age and growth

The relationship between whole wet body weight (W) and standard length (SL) was described for both species by performing a log-linear power function regression on these two variables (Table 1). For both species, weight is approximately a cubic function of standard length, indicating nearly isometric growth. The similarity in parameter estimates (Table 1) is consistent with the morphological similarity of these two species. Linear regressions were performed to permit conversion between standard, fork, and total lengths (Table 1).

Otolith growth increments from 14 *C. melampygus* and 10 *C. ignobilis* (Table 2) were counted with the aid of SEM (Fig. 2) to estimate age (Appendix A). Assuming that increments were deposited daily, the data were fitted to the von Bertalanffy growth equation (Fig. 3) for fish SL, l_t (in millimeters), as a function of age, t (in years),

$$l_t = L_\infty (1 - e^{-K(t-t_0)}).$$

The estimates for the parameters are shown in Table 2.

The accretion rate of otolith growth increments was measured in *C. melampygus* using six tetracycline-marked animals, held 55 days after injection. A discrete fluorescent line was discernible in all six subjects (Fig. 4), although marginal increments (developed peripheral to the line) were evident in only five. Three thin replicate sections were made from the sagittae of each, and marginal increments were enumerated, although one of the five specimens produced only two satisfactory preparations.

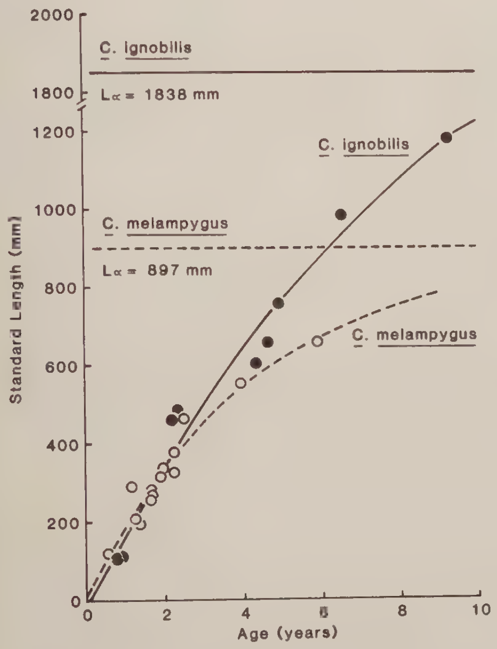

Figure 3

Growth data and von Bertalanffy growth curves derived for *Caranx melampygus* and *Caranx ignobilis*. Age was estimated by counting daily growth increments of otoliths. (See Table 2 for details.)

The 14 counts yielded a pooled mean of 51.6 marginal increments (range 47–62, SD 4.31) and a 95% confidence interval of 49.1–54.1 increments. One-way analysis of variance, however, showed that significant differences existed among the five fish in mean increment count (*F* 4.61, df 4, 9, *P* 0.027). Furthermore, variation in marginal increment deposition within specimens (s^2 8.80) was comparable to that between specimens (s^2 10.59). When mean counts of the five individual fish were compared, the 95% confidence interval for the population mean was 47.0–56.1 marginal increments. The number of days since injection (55) falls within this interval, and in general the marginal counts are reasonably close to this number.

During the maximum feeding-rate experiment, the six specimens of *C. melampygus* increased from an average standard length of 174 mm (range 166–185 mm) to 239 mm (range 225–252 mm) over a period of 161 days. This represents an average growth rate of 0.40 mm/day. An instantaneous growth rate of 0.45 mm/day (1.02 g/day) was calculated for "wild" fish within the same size range by using the von Bertalanffy growth curve.

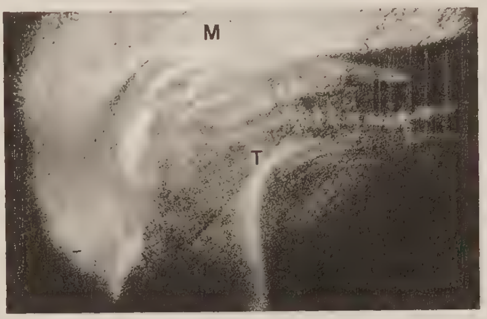

Figure 4

Ultraviolet-white light double-exposure micrograph of a section of sagitta from *Caranx melampygus*, marked for growth validation. The fish specimen had been injected with tetracycline 55 days before sacrifice. The fluorescent tetracycline mark (T) is visible as a light band inside the otolith margin (M).

Reproduction

Sex was determined in 119 specimens of *C. melampygus* and 110 specimens of *C. ignobilis*. In both species, the sex ratio of the samples, M:F, was slightly skewed toward females: 1:1.48 for *C. melampygus* (χ^2 4.45, df 1, *P* 0.04) and 1:1.39 for *C. ignobilis* (χ^2 2.95, df 1, *P* 0.08).

Using morphological criteria, gonads from 152 *C. melampygus* and 124 *C. ignobilis* were visually classified into one of three reproductive stages (immature, developing, or gravid). To test the accuracy of this visual technique, gonadosomatic indices from 62 *C. melampygus* were compared with the reproductive stages assigned visually for each fish. A two-way factorial analysis of variance, with stage (immature, developing, or gravid) and sex (male or female) as classification variables and log-transformed GSI as the dependent variable, showed that stage (*F* 44.34, df 2, 52, $P<0.0001$), but not sex (*F* 0.95, df 1, 52, *P* 0.334) affected gonadosomatic index. The interaction term was insignificant (*F* 1.69, df 2, 52, *P* 0.194). Mean values of the untransformed GSI's for the three stages of reproductive condition were 0.16%, 0.42%, and 4.54%, respectively. Sidak *t*-tests (SAS 1985) revealed that all three means were significantly different from one another. Thus, the two methods of establishing reproductive condition show a high degree of concord-

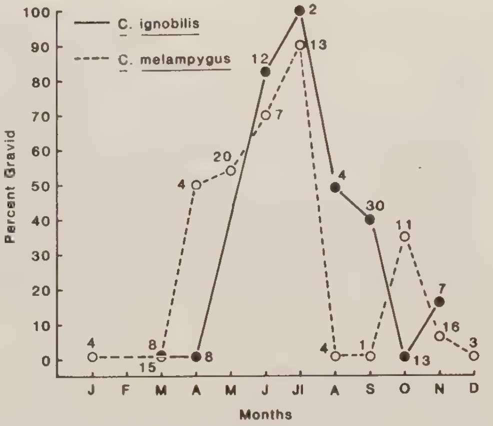

Figure 5

Percent of *Caranx melampygus* and *Caranx ignobilis* found gravid for each monthly sample available (as established by visual gonad classification). Numbers on the figure indicate individual sample sizes. Total sample sizes were 98 *C. melampygus*, all >350 mm SL, and 84 *C. ignobilis*, all >600 mm SL.

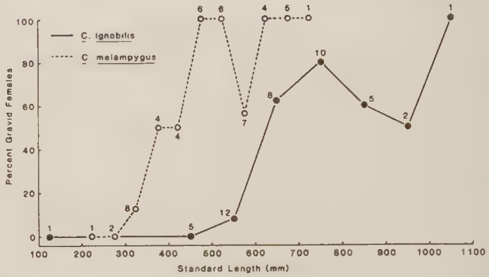

Figure 6

Size at first reproduction for female *Caranx melampygus* and *Caranx ignobilis*. Percent of sampled females found gravid (by visual gonad classification) in each size-class is plotted against standard length. Only fish sampled during summer spawning season are included. Numbers on the figure indicate individual sample sizes. Total sample sizes were 48 *C. melampygus* and 43 *C. ignobilis*.

ance. Visual gonad stage was the variable we used most often for determining spawning season and SFR.

Of 98 mature *C. melampygus* (>350 mm SL) compared by visual gonad classification, gravid individuals were found from April to November (Fig. 5). In May, June, and July more than half the individuals were gravid. Results from April, August, and September are questionable because sample sizes were small. The GSI's were also plotted against the month of capture to determine spawning season for *C. melampygus*, with consistent results. Again June and July were the peak months, but there were no gonad samples from which GSI's could be calculated in April or May. A peak in reproductive condition was also visually observed in gonads of mature (>600 mm SL) *C. ignobilis* in summer (Fig. 5). No animals of mature age were caught in December, January, or February, but only 1 of the 36 taken from October to April was gravid.

Among 48 female *C. melampygus* caught during spawning season (April to October), first reproduction (based on visual gonad classification) appeared to occur between the 325 mm and 375 mm length-classes. In this size range, the percent of gravid individuals increased sharply from 12% to 50%, and at least 50% of all larger females were gravid during these months (Fig. 6). For 43 female *C. ignobilis* caught from May to October, there was a sharp increase from 8% to 62% gravid between the 550 mm and 650 mm length-classes (Fig. 6), and all larger length-classes had a higher incidence of gravid females. Thus, it appears that female *C. melampygus* reach sexual maturity at about 350 mm SL, and female *C. ignobilis* at about 600 mm SL.

Fecundity was estimated for *C. melampygus* from ovaries of 11 gravid females caught in July. The estimated fecundity ranged from 49,700 mature ova for a fish of 760 g (328 mm SL) to 4,270,000 for one of 6490 g (640 mm SL) (Appendix B). A log-linear power function regression was performed in which fecundity, F, in number of eggs, was compared with total wet body weight, W, in grams, and SL, in millimeters. The regression equations are:

$$F = 0.923\ W^{1.694}, \qquad (r^2\ 0.84),$$

$$F = 2.286 \times 10^{-9}\ (SL)^{5.359}, \qquad (r^2\ 0.80).$$

Diet

Of 118 guts of *C. ignobilis* examined, 68.6% contained identifiable prey items, which were subjected to qualitative and quantitative analysis (Table 3). Of the *C. ignobilis* guts with identifiable prey items, 80.3% contained the remains of fishes. Parrotfish (Scaridae) were the most important identified family of fish in the diet, occurring in 13.6% of the guts that contained prey. Carangids, most notably the opelu *Decapterus macarellus*, were identified in 8.6% of the guts, and wrasses (Labridae) and bigeyes (Priacanthidae) each occurred in 6.2%. Eels (Anguilliformes: Muraenidae, Congridae,

Table 3

Summary of stomach content analysis for *Caranx ignobilis* based on 81 specimens containing prey identifiable to some taxonomic level. At the highest systematic level of analysis, unidentified fish were included in the total number of prey individuals. (In addition, only numerical and frequency percents were calculated for unidentified fish, as shown within parentheses.) Unidentified fish were not included in the totals used to calculate volume percent nor in any analysis at lower systematic levels. Percentages for a few identifiable species appear within brackets [ ]; no IRI was calculated at this level. All values not underlined or enclosed were used together as a single level for analysis.

Prey item	Numerical %	Volume %	Frequency %	% of summed IRI
Fish	69.1	73.1	80.3	90.2
Scaridae	13.4	13.4	13.6	23.0
Carangidae	5.2	4.5	8.6	5.3
Decapterus macarellus	[2.2]	[2.3]	[3.7]	
Labridae	3.7	15.6	6.2	7.5
Priacanthidae	3.7	6.8	6.2	4.1
Muraenidae	6.0	4.9	6.2	4.3
Congridae	6.0	5.1	6.2	4.3
Unidentified eels	4.5	4.7	4.9	2.9
Mullidae	2.2	8.6	2.5	1.7
Parupeneus cyclostomus	[0.8]	[8.2]	[1.2]	
Pomacentridae	3.0	0.9	3.7	0.9
Ostraciidae	3.0	1.7	4.9	1.4
Monacanthidae	5.2	0.9	2.5	1.0
Acanthuridae	2.2	2.6	1.2	0.4
Holocentridae	0.8	2.9	1.2	0.3
Ophidiidae (*Brotula multibarbata*)	0.8	0.5	1.2	0.1
Unidentified fish	(24.2)	—	(44.4)	—
Crustaceans	12.9	11.0	17.3	3.3
Palinurid lobsters	3.0	10.5	3.7	3.2
Unidentified crustaceans (incl. 1 portunid crab)	14.2	0.6	13.6	12.6
Cephalopods	17.4	15.9	24.7	6.5
Squid	10.5	2.8	9.9	8.3
Octopus	11.2	12.5	12.4	18.4
Unidentified cephalopods	1.5	0.6	2.5	0.3
Gastropods (*Bittium parcum*)	0.6	—	1.2	<0.05

and unidentified) were found in 14.8% of the guts, cephalopods in 24.7%, and crustaceans (including lobsters, crabs, and shrimp) in 17.3%.

Of 147 guts of *C. melampygus* examined, 85.0% contained identifiable prey items (Table 4), and 96.0% of these contained the remains of fish. The wrasses (Labridae), goatfish (Mullidae), filefish (Monacanthidae), damselfish (Pomacentridae), parrotfish (Scaridae), and bigeyes (Priacanthidae) were the most important families of fishes in the diet of *C. melampygus*. Eels and cephalopods made negligible contributions. Crustaceans of many diverse groups were found in 19.2% of the guts with identifiable prey items, but they accounted for less than 1% of total prey volume. Palinurid lobsters were absent.

Comparison of the diets of the two length categories of *C. melampygus* showed only one significant difference. Crustaceans were found in 17 of 42 guts from fish of the smaller length category (<350 mm SL), but in only 7 of 107 guts from the larger length category (>350 mm SL). This indicates a statistically significant (χ^2 21.5, df 1, $P<0.001$) change in the diet of *C. melampygus* with size.

The Pianka (1973) index of overlap, used to measure the degree of similarity in the diets of the two carangids, was calculated from the proportional IRI representation (% of summed IRI) for each prey group found in the two species. The value of A_{yz} was 0.42.

Maximum feeding rates were determined for six captive juvenile *C. melampygus*. These fish started at a mean weight of 124.5 g, and during the course of the

Table 4

Summary of stomach content analysis for *Caranx melampygus* based on 125 specimens containing prey identifiable to some taxonomic level. At the highest systematic level of analysis, unidentified fish were included in the total number of prey individuals. (In addition, only numerical and frequency percents were calculated for unidentified fish, as shown within parentheses.) Unidentified fish were not included in the totals used to calculate volume percent. No unidentified animals from any major taxonomic group were used in any analysis at lower systematic levels. Percentages for some identifiable genera and species appear within brackets [ ]; no IRI was calculated at this level. All values not underlined or enclosed (except Caridea) were used together as a single level for analysis.

	Numerical %	Volume %	Frequency %	% of summed IRI
Fish	85.4	98.7	96.0	98.66
Labridae	18.1	13.0	23.2	36.4
Bodianus bilunulatus	[0.5]	[1.0]	[0.8]	
Thalassoma spp.	[3.8]	[2.8]	[4.8]	
Xyrichtys spp.	[1.9]	[1.7]	[1.6]	
Mullidae	7.1	17.7	12.0	15.0
Parupeneus multifasciatus	[1.9]	[8.0]	[3.2]	
P. cyclostomus	[0.5]	[3.5]	[0.8]	
Monacanthidae (*Pervagor* spp.)	13.3	7.4	12.0	12.5
Scaridae	6.2	19.0	8.0	10.2
Pomacentridae	7.1	9.4	10.4	8.7
Stegastes fasciolatus	[1.0]	[0.7]	[1.6]	
Chromis spp.	[2.4]	[5.0]	[2.4]	
Priacanthidae	5.2	16.0	6.4	6.8
Acanthuridae	2.9	6.7	4.0	1.9
Acanthurus nigroris	[0.5]	[4.9]	[0.8]	
Naso unicornis	[1.0]	[0.4]	[0.8]	
Synodontidae	2.9	2.0	4.8	1.2
Holocentridae	2.9	1.2	3.2	0.7
Flammeo sammara	[0.5]	[0.5]	[0.8]	
Belonidae	1.0	3.7	1.6	0.4
Kyphosidae	1.4	0.4	2.4	0.2
Pomacanthidae (*Centropyge potteri*)	1.0	0.8	1.6	0.15
Blenniidae	3.3	0.1	0.8	0.14
Ophichthidae	1.0	0.2	1.6	0.1
Muraenidae	0.5	0.5	0.8	0.04
Unidentified eels	0.5	0.2	0.8	0.03
Gobiidae	1.0	—	0.8	>0.04
Tetraodontidae	1.0	0.1	0.8	0.04
Scorpaenidae	0.5	0.2	0.8	0.03
Bothidae	0.5	—	0.8	>0.02
Unidentified flatfish	0.5	0.1	0.8	0.02
Unidentified fish	(34.8)	—	(44.0)	—
Crustaceans	11.2	0.9	19.2	1.3
Shrimp	9.0	0.4	9.6	4.6
Caridea (incl. *Alpheus*, *Saron* and *Rhynchocinetes* spp.)	2.9	0.14	4.8	
Crabs (incl. Portunidae and other Brachyura)	1.9	0.14	3.2	0.3
Stomatopods	2.4	0.14	3.2	0.4
Pseudosquilla ciliata	[1.4]	[0.06]	[1.6]	
Pseudosquilla oculata	[1.0]	[0.08]	[1.6]	
Isopods	0.5	—	0.8	>0.02
Cephalopods	0.6	0.4	1.6	0.01
Octopus	0.5	0.4	0.8	0.04
Gastropods (incl. *Bittium impendens*, *Vitricithna marmorata*, and *Modulus tectum*)	2.8	—	2.4	>0.04

161-day experiment, grew to a mean weight of 302.5 g. All fish survived and appeared healthy throughout the course of the feeding experiment. Four intensive feeding periods of 6, 6, 4, and 5 days duration resulted in an average daily food consumption rate of 0.084 g food per gram of fish. Three *C. ignobilis* specimens of about 500 g each were used in a similar experiment. Three intensive feeding periods with these fish resulted in an average daily food consumption rate of about 0.05 g food per gram of fish. However, this estimate is probably low because these experimental fish seemed to be in poor health during confinement.

Energy budget and population consumption

Based on the captive feeding experiments with *C. melampygus*, an estimate of $\alpha = 0.19\,g^{0.2}$/day (at about 24°C) was derived and used for all energy budget calculations for both species. Estimates of all major components of the energy budget were calculated for the 38 weight-classes of *C. melampygus* (ranging from 200 to 10,000 g) and the 71 weight-classes of *C. ignobilis* (ranging from 500 to 41,000 g) represented in the size-frequency database. Table 5 contains selected

Table 5

Computed major components of an estimated energy budget for *Caranx melampygus* and *Caranx ignobilis* in the Northwestern Hawaiian Islands. Values are selected for various sizes within the full range of the size distribution (26 additional size-classes for *C. melampygus* and 55 for *C. ignobilis* are not shown). All energy rates are expressed in equivalent grams of fish tissue.

1	2	3	4	5	6	7	8	9
Weight class (g)	SL (mm)	Age (yr)	Growth rate, G (g/day)	Respiratory metabolic rate, Q (g/day)	Reproductive production rate, S (g/day)	Individual ration, C (g/day)	Fraction of population	Proportional ration of weight class* (g/year)
				Caranx melampygus				
200	200	1.05	1.29	13.17	0	18.08	0.057	375
1000	344	2.06	3.01	47.72	0	63.42	0.053	1223
1200	366	2.23	3.26	55.22	0.33	73.52	0.041	1091
2000	434	2.83	4.01	83.09	0.55	109.57	0.024	975
3000	498	3.47	4.56	114.93	0.82	150.39	0.016	892
4000	548	4.05	4.85	144.68	1.09	188.28	0.041	2794
5000	591	4.61	4.97	172.95	1.37	224.12	0.0081	665
6000	628	5.16	4.97	200.11	1.64	258.40	0.0041	383
7000	662	5.71	4.86	226.38	1.92	291.45	0.0041	432
8200	698	6.40	4.63	256.92	2.25	329.75	0.012	1468
9000	720	6.89	4.43	276.79	2.46	354.60	0.0041	526
10000	746	7.53	4.12	301.13	2.74	384.98	0.0041	571
Total (including weight classes not shown) = ration of individual representative of population =								47,815
				Caranx ignobilis				
1000	367	2.10	3.82	47.72	0	64.44	0.019	447
2000	458	2.68	5.75	83.09	0	111.06	0.037	1490
3000	521	3.10	7.24	114.93	0	152.72	0.058	3250
4000	571	3.45	8.47	144.68	0	191.44	0.018	1240
5000	613	3.75	9.53	172.95	1.37	229.82	0.014	1169
6000	650	4.03	10.47	200.11	1.64	265.29	0.011	1104
7000	682	4.28	11.31	226.38	1.92	299.51	0.024	2632
8000	712	4.51	12.07	251.90	2.19	332.70	0.032	3848
9000	739	4.73	12.76	276.79	2.46	365.02	0.030	4053
10000	764	4.94	13.40	301.13	2.74	396.59	0.027	3853
15000	870	5.87	15.93	416.51	4.11	545.69	0.021	4291
20000	953	6.69	17.71	524.30	5.48	684.35	0.011	2849
25000	1024	7.43	18.98	626.77	6.85	815.74	0.011	3396
30000	1085	8.14	19.87	725.19	8.22	941.60	0.0025	871
35000	1140	8.81	20.47	820.37	9.59	1063.03	0.0013	492
41000	1198	9.61	20.87	931.07	11.23	1203.97	0.0013	557
Total (including weight classes not shown) = ration of individual representative of population =								150,686

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* Product of Columns 7 and 8, adjusted to annual basis.

Table 6

Annual consumption (ration) of entire estimated populations of *Caranx melampygus* and *C. ignobilis* at French Frigate Shoals (FFS) and predation on major prey categories.

Estimated total population at FFS	Ration of individual representative of population* (kg/yr)	Breakdown by prey category**			Total consumption by population (t/yr)
		Prey category	Volume % (from Tables 3 and 4)	Consumption of prey category (t/yr)	
Caranx melampygus					
230,000	47.82				11,000
		Fish	98.7	10,854	
		Crustaceans	0.9	99	
		Cephalopods	0.4	44	
Caranx ignobilis					
130,000	150.69				19,600
		Fish	73.1	14,320	
		Crustaceans	11.0	2,155	
		Cephalopods	15.9	3,115	
Both species combined					
360,000					30,600
		Fish		25,174	
		Crustacens		2,254	
		Cephalopods		3,159	

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*From Table 5

**Volume percent for gastropod prey was not measured; amounts were negligible compared with the other three categories.

values covering the full range of sizes, with energy rate terms expressed in fish tissue gram equivalents. Age and standard length were computed from the von Bertalanffy model, and energy components were calculated as described in the Methods section. Entries within a row in Columns 1–7 are all raw, unweighted values for an individual of a particular weight-class. Thus, Column 7 contains the estimated ration of a weight-class. In Column 9, this value is weighted by the fraction (Column 8) which that weight-class contributes to the total population. Thus, for *C. melampygus* the sum of all 38 "proportional ration" values such as the examples in Column 9 constitutes the ration of a hypothetical individual representative of the entire population, i.e., 47.82 kg/year of prey. Similarly, for *C. ignobilis* the sum of all 71 "proportional ration" values provides the annual ration of such a representative individual, i.e., 150.69 kg/year.

The best estimates of species populations for FFS that our census data permit are about 230,000 *C. melampygus* and 130,000 *C. ignobilis* (Table 6). Combined with the estimate of annual ration of the representative individual of each species, these values produce estimates of total annual consumption of about 11,000 metric tons (t)/year by *C. melampygus* (about 22 t/year per km^2 of prime habitat), and about 19,600 t/year by *C. ignobilis* (about 39.2 t/year per km^2). Table 6 shows the annual amount eaten of each major prey category, based on results in Tables 3 and 4.

Discussion

Age and growth

Length-weight data for these species have been previously reported. Seki (1986a) reported a power function regression based on 124 *C. ignobilis* specimens caught in the Northwestern Hawaiian Islands, ranging in FL from 207 to 1330 mm. Applying the FL–SL relationship of Table 1 to his result produced the expression,

$$W = 3.44 \times 10^{-5} (SL - 6.0)^{2.913}.$$

Over the range of sizes collected in both studies, predictions of W from this relationship and that of Table 1 (based on 118 NWHI specimens) agree within about 7% at worst, and for a large majority of the specimens they agree within 2–5%. Their predictions are most divergent (over 8.5%) as L_∞ is approached.

Seki (1986b) also reported an expression for FL versus weight based on only 24 specimens of *C. melampygus*, 93–710 mm FL. Applying the FL–SL relation of Table 1 to this result produced the expression,

$$W = 3.0053 \times 10^{-5} (SL - 1.5)^{2.941}.$$

The agreement between predictions of this expression and those of Table 1 (based on 149 NWHI specimens) is much poorer. Over the range collected in both studies, the relationship from Seki predicts W values 14.5–17% lower than our estimates; near L_∞, the difference is almost 18%. The larger difference compared with that for *C. ignobilis* may be due to the small sample size for one *C. melampygus* regression.

Williams (1965) also fitted a length-weight expression based on 75 *C. melampygus* specimens from east Africa. Converted to common units (SL in millimeters, W in grams), his relationship is

$$W = 1.4173 \times 10^{-5} SL^{3.066}.$$

Over the range of sizes occurring in both studies, this expression predicts weights 10–17% lower than ours and closer to those of Seki (1986b). Near L_∞ it is within 8% of our estimates, and for our smallest specimens its estimates are about 27% lower. The large differences between predictions of Williams' model and ours may reflect a difference in body proportions or in large-scale "condition factor" between this species in the NWHI and east Africa. Or the result may simply be an artifact of sampling. Williams (1965) commented that in his sample, males were probably larger on average and more variable in weight than females. The ratio of males to females was much larger in his sample than in ours.

Uchiyama et al. (1984) fitted length-weight data for *Seriola dumerili* and *Pseudocaranx dentex* from the NWHI to power functions. For all four of these large, closely related species, the data fit a power function model well and the parameter values are similar.

Uchiyama and Tagami (1984) reported a preliminary von Bertalanffy growth equation for *Seriola dumerili* based on counts of daily otolith increments up to about 2 years of age (well below the inflection point of the von Bertalanffy weight curve). These results show a faster initial increase in size early in life in *S. dumerili* than in either *Caranx* species. The K values for both *Caranx* species fall well within the range of common values for many large fishes.

For both *Caranx* species, our counts of otolith growth increments made with an SEM gave estimates of age that could be fitted well to the von Bertalanffy age-length model. The daily nature of increment deposition was partly validated for *C. melampygus* by the tetracycline marking experiment. Caution must be used in extrapolating the one-to-one correspondence to fish larger than those used in the validation experiment. Recent work has shown that growth increments in the otoliths of older fish may be deposited at intervals greater than one day (Pannella 1971, Wild and Foreman 1980, Ralston and Miyamoto 1983). If so, age would be underestimated and growth rate would be overestimated.

The close agreement between the growth rate measured for captive *C. melampygus* fed *ad libitum* and the natural rate estimated from the von Bertalanffy growth curve may be fortuitous. There are a number of aspects of the captive situation that might be expected to create disparity between these results. Even though the fish were fed at least daily to satiation, the confined tank environment and human disturbance may have affected their behavior or health and slowed their growth. These fish are wide-ranging active predators, and the laboratory tank provides an unnatural environment for feeding and metabolism. A limitation of the captive feeding study was that only young, fast-growing, sexually immature specimens were available. It is not clear that the growth pattern or metabolic parameters estimated from these experiments are fully applicable over the life span of the fish. Relative growth and ingestion rates are high at younger ages, and otolith ring deposition is more likely to be daily. It would be useful, but technically difficult, to perform these experiments with large adults.

The von Bertalanffy relationship obtained for *C. ignobilis* predicts a value of $SL_\infty = 1838$ mm, and (by use of our length-weight regression) $W_\infty = 120.14$ kg. By comparison, the largest *C. ignobilis* specimens reported caught in Hawaii (with length estimates based on our regression) are 86.71 kg (1648 mm), 81.49 kg (1613 mm), and two specimens of 68.10 kg reported as measuring about 1524 mm and 1626 mm FL, respectively (about 1417 mm and 1512 mm SL, on the basis of our regressions) (Chuck Johnston, Editor, Hawaii Fishing News, Honolulu, pers. commun.). All these reports are from the main, inhabited Hawaiian islands and reflect recent conditions, following several decades of heavy fishing pressure on the species. Larger specimens may occur in the relatively unfished NWHI, where stocks are in near virgin condition and sampling has been sparse.

For *C. melampygus*, the predicted $SL_\infty = 897$ mm and $W_\infty = 17.31$ kg. Catch records from the fishery are not well documented. However, there are reliable reports of a *C. melampygus* caught on Oahu that weighed just over 19 kg and one caught on Lanai that weighed about 13.6 kg (Peter Dunn-Rankin, Univ. Hawaii, Honolulu, pers. commun.). The largest specimen for which we found documented record was one of our own: SL = 760 mm, W = 10.00 kg. From sizable collections by the Hawaii Division of Aquatic Resources and by the National Marine Fisheries Service, the largest specimens reported (with length estimates based on our regression) were 8.20 kg (698 mm) and 6.40 kg (642 mm), respectively. For both these jack species, the values of L_∞ and W_∞ derived from our size-age data are close to or somewhat greater than reported values.

Reproduction

The sex ratios for both species were skewed slightly toward females. The deviation from unity was not highly significant, and the difference may be merely a sampling artifact. Off the coast of east Africa, Williams (1965) reported overall sex ratios significantly biased toward males for both *C. melampygus* (M:F 1.68:1, *N* 78) and *C. ignobilis* (M:F 2.01:1, *N* 323). Males also predominated in an earlier series of collections there (Williams 1956). Off Zanzibar Island (east Africa) during the summer spawning season, he reported encountering shoals of "ripe and running" *C. ignobilis* composed almost entirely of males. He also sampled shoals where only females were caught and suggested that the sexes segregate in the prespawning period. Our catch data indicate that disproportionate numbers of gravid females were taken from large schools during summer. This behavior suggests that spawning by *C. ignobilis* is not a random process, but is coordinated in space and time. Whether or not large numbers of males and females aggregate to spawn is unknown, but seems likely.

Based on the data in Figure 5, it appears that both species spawn primarily in summer. However, the paucity of quantitative gonad data (e.g., GSI's) makes it difficult to present a complete picture of the annual reproductive cycle for either species. A review of the spawning patterns of Hawaiian fishes by Walsh (1987) suggested that most Hawaiian reef fishes spawn primarily during summer.

Based on the condition of gonads examined in the field, Williams (1956, 1965) concluded that spawning of *C. ignobilis* off east Africa (1°S–10°S lat.) occurs from July to March, peaking in November to March (the austral summer). He reached no conclusions about seasonality of spawning in *C. melampygus*, but he documented ripe gonads throughout the austral spring and summer (September to March).

Based on visual underwater observations of spawning behavior between Cebu and Bohol in the Philippines (10°N lat.), von Westernhagen (1974) concluded that the main spawning season of *C. ignobilis* was December and January, with a lesser peak in June. "Limited but noticeable" behavioral spawning activity was reported throughout the year for a group of carangid species that included *C. ignobilis*, but it is not clear in what months *C. ignobilis* specifically was observed spawning. This seasonal trend based on observed behavior at low northern latitudes differs from the trend indicated at higher latitudes by our examination of gonads. Von Westernhagen also found that gonads of dissected specimens were always only partly ripe, suggesting serial spawning over a prolonged seasonal period.

In our study, female *C. melampygus* became sexually mature at about 350 mm SL, which is about 39% of L_∞. The calculated age of a 350 mm *C. melampygus* is close to 2 years. Female *C. ignobilis* mature at about 600 mm SL, about 33% of L_∞, at an estimated age of about 3½ years.

Williams (1965) estimated that the onset of sexual maturity in *C. melampygus* in east Africa occurred at about 30–40 cm (apparently SL). The basis of this estimate is not clear, but it agrees well with our results for the NWHI. In southern Africa, van der Elst (1981) indicated that maturity in this species occurred at 40 cm FL (source of information not stated). From plots of standard length and weight frequency of more than 330 *C. ignobilis*, Williams (1965) surmised that maturity was reached between 54 and 61 cm (apparently SL), and between about 3 and 5 kg. Both this length and weight estimate are consistent with our results. Van der Elst (1981) stated that "sexual maturity coincides with a fork length of 60 cm and an age of approximately 3 years."

Fecundity in our study was estimated only for *C. melampygus*. The equation relating fecundity to weight suggests a strongly nonlinear increase in fecundity with increasing body weight. *Caranx melampygus* appears to be a highly fecund species with a profligate reproductive pattern common to many pelagic marine fishes.

Diet

The diet of *C. ignobilis* contained a considerable diversity of fish types and invertebrates (Table 3). The perciform and tetraodontiform fishes were very important, but eels, crustaceans, and cephalopods were also significant in numbers and volume. The large number of reef fishes suggests that *C. ignobilis* spends much of its time foraging over shallow-water reef habitats, but the presence of squid and the schooling carangid *Decapterus macarellus* indicates exploitation of more open-water habitats as well. Diet results of Williams (1965) from east Africa also indicate feeding at all levels in the water column and probably over a variety of substrates. The presence in the diet of nocturnally active species such as eels, lobsters, and octopus suggests at least partly nocturnal feeding habits. Okamoto and Kawamoto (1980) concluded that *C. ignobilis* "appeared to be primarily a night feeder" in the NWHI. Van der Elst (1981) characterized this species in southern Africa as "more active during the day, especially at dusk and dawn."

C. melampygus appears to be more dependent on diurnally active, shallow-water reef fishes (Table 4). The labrids, mullids, pomacentrids, scarids, and monacanthids, which made up over 80% of its diet (percent of summed IRI), are among the more common reef fishes in the NWHI (Parrish et al. 1985). No deep-water or pelagic species were represented in the diet, which suggests that *C. melampygus* associates closely with shallow-water reefs. The relatively low incidence of nocturnally active prey items suggests that this species is primarily a diurnal or crepuscular feeder. Based on their studies in the NWHI, Okamoto and Kawamoto (1980) also believed that it feeds mostly diurnally. On Hawaii Island, Hobson (1974) concluded that it probably feeds most often during early morning and late afternoon. In southern Africa, van der Elst (1981) stated that "while most active during early morning and late afternoon, it also hunts at night."

Little information is available on the diets of these two *Caranx* species in Hawaii or elsewhere. Okamoto and Kawamoto (1980) made the following brief, summary report, based on examination of the guts of 104 *C. ignobilis* and 27 *C. melampygus* from the NWHI: "Stomach contents of (*C. ignobilis*). . .included spiny and slipper lobsters, shrimps, portunid crabs, octopuses (*Octopus cyanea* and *Octopus ornatus*), eels, cornetfish, squirrelfishes (family Holocentridae), and surgeonfishes. The omilu (*C. melampygus*) on the other hand, was primarily a diurnal fish feeder with piha (*Spratelloides delicatulus*) comprising the bulk of its diet." Small, incidental collections of *C. melampygus* guts at South Kona (Hobson 1974, five specimens with prey) and South Kohala (Parrish, unpubl. data, three specimens with prey) on the west coast of Hawaii Island contained fishes, shrimp, stomatopods, and mysids.

Only fishes (including the serranid *Anthias* and a carangid) were found in the guts of four *C. melampygus* examined by Randall (1955) from the Gilbert Islands and two specimens examined by Hiatt and Strasburg (1960) from the Marshall Islands. Randall (1980) also reported on fish prey in the guts of 44 specimens of *C. melampygus* from the Marshall Islands, Hawaiian Islands, Line Islands, Marcus Island, Solomon Islands, and the Red Sea. Prey groups included eels, Caracanthidae, Serranidae (*Anthias* spp.), Priacanthidae, Carangidae, Caesionidae, Mullidae, Pomacentridae, Cirrhitidae, Labridae, Gobiidae, Acanthuridae, and squid. He also found food in the guts of seven specimens of *C. ignobilis* from the Marshall Islands, Line Islands, Hawaiian Islands, Pitcairn Group, and the Marquesas (Randall 1980). Prey included Scorpaenidae, Scaridae, and Acanthuridae.

Off east Africa, Williams (1956, 1965) reported only the percent of *C. ignobilis* specimens that contained each prey category (frequency percent) from 170 specimens that contained identifiable prey. His results included eels (0–2%), Synodontidae (0–1%), Plotosidae (0–1%), Belonidae (*Tylosurus* sp.) (1–2%), *Atherina* sp. (1–2%), Carangidae (0–2.5%), Leiognathidae (0–1%), Sphyraenidae (0–1%), Scaridae (2.5–6%), *Siganus* sp. (1–2%), Monacanthidae (0–1%), Tetraodontidae (0–1%), shrimp (0–2%), stomatopods (including *Squilla* sp.) (6–10%), and cephalopods (including squid) (2.5–4%). Including many unidentified prey groups, 79–84% of *C. ignobilis* contained fish, and at least 12% contained crustaceans. Similar analysis of 89 *C. melampygus* specimens containing prey (Williams 1956, 1965) indicated the following frequency percent for prey categories: Holocentridae (0–3%), Scorpaenidae (0–2%), *Caesio* spp. (2–13%), Lutjanidae (including *Lutjanus* sp.) (2–3%), Mullidae (0–2%), Labridae (0–2%), Scaridae (5–7%), and stomatopods (0–2%). Altogether, 97–100% of these specimens contained fish (many unidentified).

Based on all available results, the diets of both *Caranx* species appear to be strongly dominated by fishes; *C. melampygus* was considerably more limited to fishes in our study. Both jacks ate a wide variety of species and ecological types of fishes. In both, the labrids, scarids, mullids, and priacanthids were among the most important prey, and pomacentrids and monacanthids were at least moderately abundant. All these families except monacanthids were reported in the earlier studies of the diet of *C. melampygus*.

Scarids occurred more widely and abundantly in the diets than any other fish family. This result may be biased by the ease of identifying scarid dental plates among digested fish remains. No scarids could be identified to lower taxa. Scarids may be somewhat more important to *C. ignobilis*. Labrids were important by all measures in our study (especially for *C. melampygus*) but less prominent in the reports of others. Eels were rather widely reported in the diets of both species. At least two eel families were represented in each species in our studies (a total of three eel families). Their considerable abundance in *C. ignobilis* suggests frequent, active feeding close around reef structures or other substrates that provide good cover. Seven *C. ignobilis* individuals in our study contained more than one eel each; one contained both a muraenid and a congrid eel.

Monacanthids probably are taken commonly by these jacks when monacanthid densities are normal. However, the heavy consumption indicated by our data is probably a result of an unusual population explosion of the filefish *Pervagor spilosoma* that occurred during the course of the study. The monacanthids in *C. ignobilis* were not further identifiable, but 24 of 28 monacanthid individuals in *C. melampygus* were identified as *P. spilosoma* and the other four as the genus *Pervagor*. Fourteen of the 15 incidents of predation (involving 27 of 28 prey individuals) occurred between late June 1982 and late March 1983 (when field work ended). These incidents began with the first sizable collections of jacks after the surge in the filefish population was initially observed in visual censuses. Census counts of *P. spilosoma* remained high to the end of the study. This temporal pattern of predation and prey abundance appears to offer an example of opportunistic feeding on sporadically abundant prey. The much higher incidence of *P. spilosoma* in *C. melampygus* appears to reflect the specific locations and timing of sampling relative to the filefish population surge.

Potts (1980) analyzed the predatory behavior of *C. melampygus* at Aldabra Atoll (Indian Ocean). His observations indicated that this species sometimes forages in small groups, but that it is most often found singly or in pairs. Major (1978), who conducted an investigation of the predator-prey interactions of a captive group of juvenile *C. ignobilis* in Kaneohe Bay, Hawaii, showed that there are advantages to group hunting of schooling fish. *Caranx* species are known to form interspecific feeding associations with large labrids and other predatory species such as sharks, barracuda, sting rays, and eagle rays (Potts 1980). *C. melampygus* sometimes follow species that disturb the substrate, causing small fishes and crustaceans to be flushed out and exposed (Hobson 1974; pers. observ.). Some of the small crustaceans and gastropods found in the guts of *C. melampygus* may have been taken in this way.

Potts described *C. melampygus* as a diurnally active predator that increased hunting activity at dawn and dusk, when small midwater planktivorous fishes are moving to or from the shelter of the reef. These observations are generally consistent with our analysis of the feeding habits of this species in Hawaii. However, nocturnal fishes and crustaceans occurred in some of our samples, and planktivorous fishes did not dominate the diet.

The total incidence of benthic invertebrate prey in our specimens was considerable: 43% (frequency) for *C. ignobilis* and 22% for *C. melampygus* (including all cephalopods). *Caranx ignobilis* is one of the few fishes known to consume large, fully adult lobsters (Gooding 1985). Lobsters occurred in about 4% of the specimens, composing over 10% of the diet by volume in our study (Table 3). Okamoto and Kawamoto (1980) also reported this interaction, and Gooding (1985) observed such predation in the field. Lobsters are large, long-lived invertebrates that appear to be situated high in the benthic trophic system. This is one of several links that suggests that these large, abundant *Caranx* species, with their high rates of food consumption, are particularly important apex predators (Table 6).

Large crustaceans occur rather widely in the diets reported for *C. ignobilis* and *C. melampygus* (Williams 1956 and 1965, Hobson 1974, Okamoto and Kawamoto 1980, Parrish unpubl. data). In our study, the frequency of occurrence and numerical percent of crustaceans in the diet were sizable, but the low volumes for groups other than lobsters suggest that their dietary role is quantitatively minor (Tables 3 and 4). Many crustaceans could not be identified to low taxonomic level, but the major groups found in these *Caranx* species appear to be among those most common in the diets of a wide range of other carnivorous, demersal fish species in the NWHI, e.g., shrimp, crabs, and stomatopods (Parrish et al. 1985). All these major groups have also been reported in other diet studies of these jacks.

The higher incidence of crustaceans in smaller individuals of *C. melampygus* in our study was not obviously related to characteristics of the habitat or social structure. Fish of many sizes (larger and smaller than 350 mm SL) overlapped broadly among habitats, both in our collections of specimens and in many field observations. Benthic sampling in the NWHI suggested that large crustaceans were widely available in most of these types of habitats. No direct evidence is available to confirm the basis of this size difference in diet of *C. melampygus*; it may reflect changing food preference with age and the ability of larger individuals to capture larger fish as prey. (All the crustaceans found in *C. melampygus* specimens of all sizes could probably have been captured easily by even the smallest of the specimens.)

In our study, *C. ignobilis* consumed both the benthic/demersal octopus and the more pelagic squid in quantities (Table 3) that suggest that this trophic interaction is ecologically important to predator and prey populations. Only two specimens of *C. melampygus* contained cephalopods. There have been occasional previous reports of cephalopods in these jack species (Williams 1956, Okamoto and Kawamoto 1980, Randall 1980).

There was a relatively low overlap of specific diet items between *C. ignobilis* and *C. melampygus* (index $A_{yz} = 0.42$), indicating some separation of feeding niches of these two sympatric congeners. Morphologically, they are very similar, but a mature *C. ignobilis* is considerably larger than a mature *C. melampygus*. This difference in body size probably accounts for the occurrence or higher incidence of larger prey individuals and some larger species (e.g., lobsters, octopus) in *C. ignobilis*.

Energy budget and population consumption

Preliminary energy budget calculations and estimates of food consumption were made for jack populations primarily for their ecological interest. Clearly, the estimates of energy budget terms are crude and may be of limited value from a physiological perspective.

Measured ration of fish feeding *ad libitum* while swimming actively in a relatively undisturbed captive environment was used as an estimate of the natural, long-term, average ration of fish in the wild. If feeding were not reduced by trauma or behavioral effects of captivity, such feeding should provide an estimate of maximum natural ration, given superabundant, easily accessible food. Since the measured growth rate in captivity closely approximated the growth rate estimated for wild fish by the von Bertalanffy model, it may be that the effects of captivity depressed the *ad libitum* feeding activity from the maximum rate, to approach the natural, long-term, average rate. In any case, there is no clear direction of bias and no obvious way to improve the estimate of natural ration.

For the parameters k and γ, there seem to be no data specifically for these jacks or for closely related species. Published values for a considerable number of rather large, active, perciform fishes are similar to those chosen in this study (about 0.8 for both parameters) (e.g., Winberg 1956). The value of k chosen affects the entire calculation of captive α and subsequently of C for all weight-classes. The value of γ affects the entire calculation of captive α, but affects only one term (the largest) in the subsequent calculation of C. For each of these parameters, because it occurs in the calculation of captive α and subsequently of C, the effects of any inaccuracy in the choice of the value tend to cancel.

Use of a single value of α for all sizes of fish introduces another assumption. In previous work, this coefficient has often been treated as constant over a considerable range of sizes (Winberg 1956). However, for most species, α has not been determined for large sample sizes or large size ranges. A rather extreme range of sizes is included in the present calculations. No adequate measurements were available to produce a direct estimate of α for *C. ignobilis*. The use in its place of the α calculated for *C. melampygus* represents an approximation, and thus the estimated components of the energy budget for *C. ignobilis* may be less reliable. However, the similarity of α values presented by Winberg (1956) for a wide variety of less closely related species suggests that the approximation used is acceptable. Temperatures in the seawater feeding tanks were close to normal sea temperatures throughout the year, and therefore no correction of α for temperature seemed necessary. (The full annual range of tank and sea temperatures was small.)

The quality of the estimate of growth rate depends upon the quality of the fitted von Bertalanffy model as a descriptor of actual growth. Both regressions were good fits, and t_0 and L_∞ values were realistic. The use of dW/dt, evaluated for each chosen weight-class, is probably the best estimate of growth rate available from the von Bertalanffy model.

The estimate of reproductive output is crude, but little else is available. Since whole body weights were used in the von Bertalanffy model regressions, at least part of the reproductive energy may be viewed as included in the growth rate term, G (on some sort of average basis across all specimens and seasons). However, since the development of reproductive products is seasonal, it seemed reasonable to add a term representing the weight of a fully developed gonad to represent additional annual reproductive energy demand. The effects from both these terms may somewhat overestimate reproductive demand. However, multiple clutches may be developed over the course of a year, so the gonad weight alone may underestimate the actual reproductive energy.

As in all such energy budgets for active animals beyond the early juvenile stages, the respiratory metabolism term, Q, was dominant (see Table 5). The growth term, G, was never more than 10% of Q for the size-classes calculated here, and the reproductive term, S, was always substantially less than G. Therefore, factors affecting the accuracy of the components of Q (e.g., assumptions about the parameters α and γ) produce the greatest effects on the total estimate of the ration, C.

Components of the basic energy budget derived in this study, e.g., growth parameters (L_∞, W_∞, K, and t_0), maximum GSI, and α, should be similar in other tropical and subtropical localities where these species occur. The value of α (and corresponding metabolism and ration) can be readily adjusted for other temperatures by using Krogh's (1959) "normal curve" or corresponding mathematical functions (e.g., Winberg 1956:32, Ursin 1967:2396).

The estimate of population consumption in the specific case of FFS was of particular interest because of the extensive community trophic work done there. A mathematical trophic model of the shallow marine ecosystem there has been produced (Polovina 1984), with the biota lumped into a dozen large trophic compartments. Jacks (especially these two *Caranx* species) are major members of one of the top trophic-level compartments. Comparison of our numbers for consumption with those from the model suggests that these jacks provide an even more important trophic path than the large-scale model predicts.

The census methodology used to produce the population estimates in Table 6 was not designed to adequately census such wide-ranging, highly mobile species, and these estimates must be considered rough. They probably represent maximum estimates. No method was found to check them directly. Extrapolation of the catch data for the year 1900 from the main Hawaiian islands produced an estimated "catch" for FFS of about 44 *C. melampygus*/km^2 and 26 *C. ignobilis*/km^2.

This is an order of magnitude lower than the visual census estimates of full populations of 460/km^2 and 260/km^2, respectively. There is no basis for estimating accurately what fraction of the standing stock of either species was caught in 1900. However, there is no evidence that the fishery was immediately depleted, so it seems likely that the standing stock was several times the annual catch for each species. It seems reasonable that the actual present stock sizes at FFS are not much greater than the figures in Table 6, and they are probably not less than a third of those estimated figures.

Based on our study, it is clear that populations of these two species combined eat at least a few thousand metric tons annually at this medium size atoll (about 500 km^2 in area to a depth of about 20 m). From an ecological perspective, this must represent one of the most important top-level trophic paths in this system (and probably in many others). The estimated combined predation pressure (Table 6) by these two jacks exceeds the combined estimate for the three dominant shark species in the same system (DeCrosta et al. 1984) by a factor of about 40. This source of mortality should be considered in any quantitative examination of the population ecology of the prey groups, particularly fish, large crustaceans, and cephalopods. The diet composition results in Tables 3 and 4 permit such analysis at lower systematic levels as well.

The information now available about these two important jacks provides an outline of their life history and trophic ecology. Both species are moderately fast growing, attain large size, and live at least several years. Both mature at relatively large size (a major consideration in fishery management), have apparent high fecundity, and may reproduce for at least 4–6 years, with a pronounced seasonal spawning cycle. These jacks are highly piscivorous, but show considerable quantitative separation in their specific diets. *Caranx melampygus* is more dependent on fishes, whereas *C. ignobilis* has a more varied diet that includes large crustaceans and cephalopods. Both species have high metabolic demands and correspondingly high rates of food consumption. Large populations of these species may impose considerable predation mortality on benthic/demersal communities, particularly on fishes. These jacks are potentially of interest in many shallow-water tropical environments because of their role in community ecology as well as in local fisheries.

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Citations

Agegian, C.R.
1985 The biogeochemical ecology of *Porolithon gardineri* (Foslie). Ph.D thesis, Univ. Hawaii, Honolulu, 178 p.

Atkinson, M.J., and R.W. Grigg
1984 Model of a coral reef ecosystem. II. Gross and net benthic primary production at French Frigate Shoals, Hawaii. Coral Reefs 3:13–22.

Cobb, J.N.
1905 The aquatic resources of the Hawaiian Islands. Section III—The commercial fisheries of the Hawaiian Islands. Bull. U.S. Fish Comm. for 1903, 23:715–765.

DeCrosta, M.A., L.R. Taylor Jr., and J.D. Parrish
1984 Age determination, growth, and energetics of three species of carcharhinid sharks in Hawaii. *In* Grigg, R.W., and K.Y. Tanoue (eds.), Proc., Second symp. on resource investigations in the Northwestern Hawaiian Islands, vol. 2, p. 75–95. Misc. Rep. UNIHI-SEAGRANT-MR-84-01, Univ. Hawaii Sea Grant Coll. Prog., Honolulu.

Everhart, W.H., and W.D. Youngs
1981 Principles of fishery science. Cornell Univ. Press, Ithaca, NY, 349 p.

Everson, A.R.

1984 Spawning and gonadal maturation of the ehu, *Etelis carbunculus* in the Northwestern Hawaiian Islands. *In* Grigg, R.W., and K.Y. Tanoue (eds.), Proc., Second symp. on resource investigations in the Northwestern Hawaiian Islands, vol. 2, p. 128–148. Misc. Rep. UNIHI-SEAGRANT-MR-84-01, Univ. Hawaii Sea Grant Coll. Prog., Honolulu.

Fabens, A.J.

1965 Properties and fitting of the von Bertalanffy growth curve. Growth 29:265–289.

Gooding, R.M.

1985 Predation of released spiny lobster, *Panulirus marginatus*, during tests in the Northwestern Hawaiian Islands. Mar. Fish. Rev. 47(1):27–35.

Gosline, W.A., and V.E. Brock

1960 Handbook of Hawaiian fishes. Advertiser Publ. Co., Honolulu, 372 p.

Grigg, R.W., and R.T. Pfund (editors)

1980 Proceedings of the symposium on the status of resource investigations in the Northwestern Hawaiian Islands. Misc. Rep. UNIHI-SEAGRANT-MR-80-04, Univ. Hawaii Sea Grant Coll. Prog., Honolulu, 333 p.

Grigg, R.W., and K.Y. Tanoue (editors)

1984 Proceedings of the second symposium on resource investigations in the Northwestern Hawaiian Islands (2 vols.). Misc. Rep. UNIHI-SEAGRANT-MR-84-01, Univ. Hawaii Sea Grant Coll. Prog., Honolulu, 844 p.

Hamamoto, H.

1928 The fishing industry of Hawaii. B.A. thesis, Univ. Hawaii, Honolulu, 45 p.

Hawaii DLNR

1989 Commercial fish landings by species, State of Hawaii, calendar year 1988. State of Hawaii, Dep. Land & Nat. Resour., Div. Aquatic Resour., Honolulu, 2 p.

Hiatt, R.W., and D.W. Strasburg

1960 Ecological relationships of the fish fauna on the coral reefs of the Marshall Islands. Ecol. Monogr. 30:65–127.

Hobson, E.S.

1974 Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. Fish. Bull., U.S. 72:915–1031.

Kesteven, G.L.

1960 Manual of field methods in fisheries biology. FAO Man. Fish. Sci. 1, 152 p.

Krogh, A.

1959 The comparative physiology of respiratory mechanisms. Univ. Pennsylvania Press, Philadelphia, 172 p.

Major, P.F.

1978 Predator-prey interactions in two schooling fishes, *Caranx ignobilis* and *Stolephorus purpureus*. Anim. Behav. 26:760–777.

Mann, K.H.

1965 Energy transformations by a population of fish in the river Thames. J. Anim. Ecol. 34:253–275.

1967 The cropping of the food supply. *In* Gerking, S.D. (ed.), The biological basis of freshwater fish production, p. 243–257. John Wiley, NY.

1969 The dynamics of aquatic ecosystems. Adv. Ecol. Res. 6:1–81.

Norris, J.E., and J.D. Parrish

1988 Predator-prey relationships among fishes in pristine coral reef communities. *In* Choat, J.H., et al. (eds.), Proc. 6th Int. Coral Reef Symposium, Townsville, Australia, 8–12 Aug. 1988, vol. 2, p. 107–113. Sixth Int. Coral Reef Symp. Exec. Comm.

Okamoto, H., and P. Kawamoto

1980 Progress report on the nearshore fishery resource assessment of the Northwestern Hawaiian Islands: 1977 to 1979. *In* Grigg, R.W., and R.T. Pfund (eds.), Proc., Symp. on the status of resource investigations in the Northwestern Hawaiian Islands, p. 71–80. Misc. Rep. UNIHI-SEAGRANT-MR-80-04, Univ. Hawaii Sea Grant Coll. Prog., Honolulu.

Paloheimo, J.E., and L.M. Dickie

1965 Food and growth of fishes. I. A growth curve derived from experimental data. J. Fish. Res. Board Can. 22:521–542.

1966 Food and growth of fishes. II. Effects of food and temperature on the relation between metabolism and body weight. J. Fish. Res. Board Can. 23:869–908.

Pannella, G.

1971 Fish otoliths. Daily growth layers and periodical patterns. Science (Wash. DC) 173:1124–1127.

1974 Otolith growth patterns: An aid in age determination in temperate and tropical fishes. *In* Bagenal, T.B. (ed.), The ageing of fish, p. 28–39. Unwin Bros., Surrey, England.

Parrish, J.D.

1975 Marine trophic interactions by dynamic simulation of fish species. Fish. Bull., U.S. 73:695–716.

Parrish, J.D., M.W. Callahan, and J.E. Norris

1985 Fish trophic relationships that structure reef communities. *In* Gabrie, C., and B. Salvat (eds.), Proc. 5th Int. Coral Reef Congress, Tahiti, 27 May–1 June 1985, vol 4, p. 73–78. Antenne Museum—EPHE, Moorea, French Polynesia.

Pianka, E.R.

1973 The structure of lizard communities. Annu. Rev. Ecol. Syst. 4:53–75.

Pinkas, L., M.S. Oliphant, and I. Iverson

1971 Food habits of albacore, bluefin tuna and bonito in California waters. Calif. Dep. Fish Game Fish. Bull. 152:5–12.

Polovina, J.J.

1984 Model of a coral reef ecosystem. I. The ECOPATH model and its application to French Frigate Shoals. Coral Reefs 3:1–11.

Potts, G.W.

1980 The predatory behavior of *Caranx melampygus* in the channel environment of Aldabra Atoll. J. Zool. Soc. (Lond.) 192:323–350.

Radtke, R.L.

1987 Age and growth information available from the otoliths of the Hawaiian snapper, *Pristipomoides filamentosus*. Coral Reefs 6:19–25.

Ralston, S.

1984 Biological constraints on production and related management issues in the Hawaiian deepsea handline fishery. *In* Grigg, R.W., and K.Y. Tanoue (eds.), Proc., Second symp. on resource investigations in the Northwestern Hawaiian Islands, vol. 1, p. 248–264. Misc. Rep. UNIHI-SEAGRANT-MR-84-01, Univ. Hawaii Sea Grant Coll. Prog., Honolulu.

Ralston, S., and K.E. Kawamoto

1988 A biological assessment of Hawaiian bottom fish stocks, 1984–87. Admin Rep. H-88-8, NMFS Honolulu Lab., Southwest Fish. Sci. Cent., Honolulu, 60 p.

Ralston, S.V., and G.T. Miyamoto

1983 Analyzing the width of daily otolith increments to age the Hawaiian snapper *Pristipomoides filamentosus*. Fish. Bull., U.S. 81:523–535.

Ralston, S., and J.J. Polovina

1982 A multispecies analysis of the commercial deepsea handline fishery in Hawaii. Fish. Bull., U.S. 80:435–448.

Randall, J.E.

1955 Fishes of the Gilbert Islands. Atoll Res. Bull. 47, 243 p.

1980 A survey of ciguatera at Enewetak and Bikini, Marshall Islands, with notes on the systematics and food habits of ciguatoxic fishes. Fish. Bull., U.S. 78:201–249.

SAS Institute, Inc.

1985 SAS user's guide: Statistics. Version 5 edition. SAS Inst., Inc., Cary, NC, 956 p.

Seki, M.P.

1986a Section on *Caranx ignobilis*. *In* Uchida, R.N., and J.H. Uchiyama (eds.), Fishery atlas of the Northwestern Hawaiian Islands, p. 86–87. NOAA Tech. Rep. NMFS 38.

1986b Section on *Caranx melampygus*. *In* Uchida, R.N., and J.H. Uchiyama (eds.), Fishery atlas of the Northwestern Hawaiian Islands, p. 88–89. NOAA Tech. Rep. NMFS 38.

Shomura, R.S.

1987 Hawaii's marine fishery resources: Yesterday (1900) and today (1986). Admin. Rep. H-87-21, NMFS Honolulu Lab., Southwest Fish. Sci. Cent., Honolulu, 14 p.

Simpson, A.C.

1951 The fecundity of the plaice. Fish. Invest. Lond. Ser. 2:1–27.

Sorden, C.T.

1984 Feeding relationships of goatfishes in the Northwestern Hawaiian Islands. *In* Grigg, R.W., and K.Y. Tanoue (eds.), Proc., Second symp. on resource investigations in the Northwestern Hawaiian Islands, vol. 2, p. 296–308. Misc. Rep. UNIHI-SEAGRANT-MR-84-01, Univ. Hawaii Sea Grant Coll. Prog., Honolulu.

Sylvester, J.R.

1969 Scales of selected Hawaiian inshore fishes with a brief review of the scale method of age and growth analysis. M.S. thesis, Univ. Hawaii, Honolulu, 84 p.

Titcomb, M.

1972 Native use of fish in Hawaii. Univ. Press of Hawaii, Honolulu, 175 p.

Uchiyama, J.H., and D.T. Tagami

1984 Life history, distribution, and abundance of bottomfishes in the Northwestern Hawaiian Islands. *In* Grigg, R.W., and K.Y. Tanoue (eds.), Proc., Second symp. on resource investigations in the Northwestern Hawaiian Islands, vol. 1, p. 229–247. Misc. Rep. UNIHI-SEAGRANT-MR-84-01, Univ. Hawaii Sea Grant Coll. Prog., Honolulu.

Uchiyama, J.H., S.H. Kuba, and D.T. Tagami

1984 Length–weight and standard length–fork length relationships of deepsea handline fishes of the Northwestern Hawaiian Islands. *In* Grigg, R.W., and K.Y. Tanoue (eds.), Proc., Second symp. on resource investigations in the Northwestern Hawaiian Islands, vol. 2, p. 209–225. Misc. Rep. UNIHI-SEAGRANT-MR-84-01, Univ. Hawaii Sea Grant Coll. Prog., Honolulu.

Ursin, E.

1967 A mathematical model of some aspects of fish growth, respiration and mortality. J. Fish. Res. Board Can. 24: 2355–2453.

van Dalsen, A.P.

1977 An improved technique for subsampling eggs for fecundity studies. Fish. Bull. S. Afr. 9:6–10.

van der Elst, R.

1981 A guide to the common sea fishes of southern Africa. C. Struik Publ., Cape Town, 367 p.

von Westernhagen, H.

1974 Observations on the natural spawning of *Alectis indicus* (Ruppell) and *Caranx ignobilis* (Forsk.) (Carangidae). J. Fish Biol. 6:513–516.

Walsh, W.J.

1987 Patterns of recruitment and spawning in Hawaiian reef fishes. Environ. Biol. Fish. 18:257–276.

Wild, A., and T.J. Foreman

1980 The relationships between otolith increments and time for yellowfin and skipjack tuna marked with tetracycline. Inter-Am. Trop. Tuna Comm. Bull. 17:509–557.

Williams, F.

1956 Preliminary survey of the pelagic fishes of East Africa. Colonial Office Fish. Publ. 8, East Afr. Mar. Fish. Res. Org., Zanzibar. Her Majesty's Stationery Office, London, 68 p.

1965 Further notes on the biology of East African pelagic fishes of the families Carangidae and Sphyraenidae. East Afr. Agric. For. J. 31:141–168.

Winberg, G.G.

1956 [Rate of metabolism and food requirements of fish]. Nauchn. Tr. belorusskovo Gos. Univ. imeni V.I. Lenina, Minsk, 253 p. [Fish. Res. Board Can. Transl. Ser. 194, 1960]

Appendix A

Numbers of increments visible by scanning electron microscopy in the otoliths of various size specimens of *Caranx melampygus* and *Caranx ignobilis*, and corresponding estimated ages of specimens (assuming daily deposition of increments).

Caranx melampygus			*Caranx ignobilis*		
Length of fish (mm SL)	No. of otolith increments	Estimated age (yr)	Length of fish (mm SL)	No. of otolith increments	Estimated age (yr)
122	186	0.510	106	274	0.751
196	486	1.332	109	276	0.756
210	458	1.255	113	293	0.803
259	598	1.638	462	793	2.173
270	612	1.677	485	846	2.318
283	596	1.633	606	1580	4.329
294	423	1.159	660	1690	4.630
320	687	1.882	760	1793	4.912
328	812	2.225	985	2387	6.540
341	710	1.945	1180	3384	9.271
380	813	2.227			
468	904	2.477			
555	1435	3.932			
660	2154	5.901			

Appendix B

Estimated batch fecundity for 11 gravid female specimens of *Caranx melampygus* of various sizes.

Length of fish (mm SL)	Whole wet weight of fish (g)	Whole wet weight of ovary (g)	Est. no. of eggs in ovary
328	760	14.1	49,700
465	1985	46	284,000
502	2590	78.5	774,000
503	2724	133	987,000
514	3667	182	888,000
520	3807	224	2,600,000
596	5167	292	1,690,000
617	5650	210	1,020,000
640	6490	440	4,270,000
649	6615	223	1,540,000
654	6220	249	2,220,000

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Effects of the Avidity Bias on Survey Estimates of Fishing Effort and Economic Value

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Abstract.—This paper describes the avidity bias (the disproportionate representation of avid anglers) in intercept surveys and shows how bias-corrected estimates of mean and variance can be computed. It compares bias-corrected participation rates with actual participation rates reported by California anglers in an economic survey conducted as a mail follow-up to a random telephone canvass, and in an on-site intercept survey. Although both samples contained this bias, it was much more pronounced in the on-site survey than in the mail survey. The findings indicate that failure to correct for avidity bias results in inflated estimates of per capita fishing expenditures and consumer surplus as well as fishing effort. In general, the effect of the avidity bias on estimates of economic value depends not only on the extent of the bias, but also on the relationship between angler expenditures and avidity, and on the functional form of the travel cost model underlying estimates of consumer surplus.

Deciding upon a method for identifying potential respondents is an important first step in designing angler surveys. This decision typically involves a trade-off between cost and bias. For instance, it is possible to obtain a representative sample of anglers by means of a random telephone canvass of the general population, but the search can be relatively costly. On-site surveys usually offer a less expensive alternative, which explains why they are commonly used to identify anglers for economic surveys; but they result in samples that may be biased in several ways.

One potential source of error is the length-of-stay bias. This bias arises when selection probabilities increase with the amount of time spent at the recreational site. In an on-site survey of Wyoming campers, Nowell et al. (1988) found that trip expenditures and willingness to pay for the opportunity to see a grizzly bear were correlated with length of stay. They provided techniques for obtaining unbiased statistics from length-biased samples.

Another potential source of bias arises when avid participants (those who participate more frequently) are disproportionately represented in on-site surveys. The overrepresentation of avid anglers in a sample is referred to as avidity bias. In this paper, I describe the derivation of mean and variance estimators used to correct for avidity bias, and I present a case study that illustrates the potential effect of this bias on estimates of per capita fishing effort and economic value.

Procedures to Correct for Avidity Bias

Suppose that n' samples are drawn from the angling population, with each sample size defined as $n = 1$.[1] If these are random replacement samples, the probability of selecting angler i in any given draw will be

$$\text{Prob(random selection of angler } i) = 1/N\,; \quad (1)$$

N is the number of anglers in the population. By contrast, if the draws result in a random sample of trips rather than a random sample of anglers (as is likely to occur with an intercept survey), the probability of selecting angler i in any given draw will be

$$\text{Prob(intercepting angler } i) = T_i/T\,. \quad (2)$$

T_i = number of trips taken annually by angler i, and
$T = \Sigma^N T_j$ = total number of trips taken annually by the population.

Suppose that we want to estimate the mean value per angler of a random variable z on the basis of data collected in an intercept survey. If z is correlated with angler avidity, its arithmetic mean, computed as

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[1] When sampling probabilities are not uniform, the derivation of statistics for nonreplacement samples is considerably more complicated than for replacement samples. Thus the distinction between drawing n' samples with replacement, each sample being of size $n = 1$, and drawing a single sample of size n (nonreplacement sampling) is conceptually important.

$$\bar{z} = \sum^{n'} Z_i/n' ,$$

will be a biased estimate of the true mean $\bar{Z}$. This section describes estimators for the mean and variance of $\bar{Z}$ that correct for the avidity bias in intercept surveys. These and other statistics are discussed more thoroughly in Jessen (1978).

Mean and Variance Estimators: The General Case

If P_i is the probability of selecting individual i, then the number of individuals in the population (N), and the population total for the variable of interest

$$Z = \sum^{N} Z_i ,$$

can be estimated respectively by

$$\hat{N} = \frac{1}{n'} \sum^{n'} \frac{1}{P_i} , \tag{3}$$

and

$$\hat{Z} = \frac{1}{n'} \sum^{n'} \frac{Z_i}{P_i} . \tag{4}$$

By substituting the selection probabilities from equation (2) for P_i, equations (3) and (4) can be expressed as

$$\hat{N} = \frac{T}{n'} \sum^{n'} \frac{1}{T_i} , \tag{5}$$

and

$$\hat{Z} = \frac{T}{n'} \sum^{n'} \frac{Z_i}{T_i} . \tag{6}$$

By using (5) and (6), $\bar{Z}$ can be estimated as

$$\hat{Z}/\hat{N} = \frac{\sum^{n'} (Z_i/T_i)}{\sum (1/T_i)} . \tag{7}$$

Although $\hat{Z}$ and $\hat{N}$ are unbiased estimators of Z and N, equation (7) is not an unbiased estimator of $\bar{Z}$. The bias of ratio estimators such as in equation (7), however, becomes negligible as sample size increases (Cochran 1977).

The variance of equation (7) is

$$\begin{aligned} \operatorname{var}(\hat{Z}/\hat{N}) &= \frac{(N-1)}{Nn'} \bar{Z}^2 \left[\frac{S^2_{z/t}}{\bar{Z}^2} + \frac{S^2_{1/t}}{\bar{N}^2} - \frac{2S_{(z/t)(1/t)}}{\bar{Z}\,\bar{N}} \right] \\ &= \frac{(N-1)}{Nn'} \bar{Z}^2 \left[\frac{S^2_{z/t}}{\bar{Z}^2} + \frac{S^2_{1/t}}{1} - \frac{2S_{(z/t)(1/t)}}{\bar{Z}} \right] ; \end{aligned} \tag{8}$$

$$S^2_{z/t} = \frac{T^2}{N(N-1)} \sum^{N} \frac{T_i}{T} \left(\frac{Z_i}{T_i} - \frac{Z}{T} \right)^2 ,$$

$$S^2_{1/t} = \frac{T^2}{N(N-1)} \sum^{N} \frac{T_i}{T} \left(\frac{1}{T_i} - \frac{N}{T} \right)^2 ,$$

and

$$S_{(z/t)(1/t)} = \frac{T^2}{N(N-1)} \sum^{N} \frac{T_i}{T} \left(\frac{Z_i}{T_i} - \frac{Z}{T} \right) \left(\frac{1}{T_i} - \frac{N}{T} \right) .$$

The relative variance (the squared coefficient of variation) associated with equation (8) is

$$\operatorname{rel\,var}(\hat{Z}/\hat{N}) = \frac{N-1}{Nn'} [V^2_{z/t} + V^2_{1/t} - 2V_{(z/t)(1/t)}] ; \tag{9}$$

$$V^2_{z/t} = \frac{S^2_{z/t}}{\bar{Z}^2} , \; V^2_{1/t} = \frac{S^2_{1/t}}{1} , \text{ and } V_{(z/t)(1/t)} = \frac{S_{(z/t)(1/t)}}{\bar{Z}} .$$

Equation (8) can be estimated from a sample by

$$\widehat{\operatorname{var}}(\hat{Z}/\hat{N}) = \left[\frac{\sum^{n'} (Z_i/T_i)}{\sum (1/T_i)} \right]^2 \frac{1}{n'} \cdot \left[\frac{s^2_{z/t}}{(\hat{Z}/\hat{N})^2} + \frac{s^2_{1/t}}{1} - \frac{2s_{(z/t)(1/t)}}{\hat{Z}/\hat{N}} \right] ; \tag{10}$$

$$\begin{aligned} s^2_{z/t} &= \frac{\bar{T}^2}{n'-1} \sum^{n'} \left(\frac{Z_i}{T_i} - \frac{\hat{Z}}{T} \right)^2 \\ &= \frac{\bar{T}^2}{n'-1} \left[\sum^{n'} \left(\frac{Z_i}{T_i} \right)^2 - \frac{1}{n'} \left(\sum^{n'} \frac{Z_i}{T_i} \right)^2 \right] , \end{aligned}$$

$$\begin{aligned} s^2_{1/t} &= \frac{\bar{T}^2}{n'-1} \sum^{n'} \left(\frac{1}{T_i} - \frac{\hat{N}}{T} \right)^2 \\ &= \frac{\bar{T}^2}{n'-1} \left[\sum^{n'} \left(\frac{1}{T_i} \right)^2 - \frac{1}{n'} \left(\sum^{n'} \frac{1}{T_i} \right)^2 \right] , \end{aligned} \tag{11}$$

and

$s_{(z/t)(1/t)}$

$$= \frac{\bar{T}^2}{n'-1} \sum^{n'} \left(\frac{Z_i}{T_i} - \frac{\hat{Z}}{T}\right)\left(\frac{1}{T_i} - \frac{\hat{N}}{T}\right)$$

$$= \frac{\bar{T}^2}{n'-1} \left[\sum^{n'} \left(\frac{Z_i}{T_i} \cdot \frac{1}{T_i}\right) - \frac{1}{n'} \sum^{n'} \frac{Z_i}{T_i} \sum^{n'} \frac{1}{T_i}\right].$$

Equation (9) can be estimated by

$$\text{rel } \widehat{\text{var}}(\hat{Z}/\hat{N}) = \frac{1}{n'} [v^2_{z/t} + v^2_{1/t} - 2v_{(z/t)(1/t)}]; \quad (12)$$

$$v^2_{z/t} = \frac{s^2_{z/t}}{\bar{T}^2[(1/n') \sum (Z_i/T_i)]^2}$$

$$= \left(\frac{n'^2}{n'-1}\right) \frac{\sum^{n'} (Z_i/T_i)^2 - (1/n')\left[\sum^{n'} (Z_i/T_i)\right]^2}{[\sum (Z_i/T_i)]^2},$$

$$v^2_{1/t} = \frac{s^2_{1/t}}{\bar{T}^2[(1/n') \sum (1/T_i)]^2}$$

$$= \left(\frac{n'^2}{n'-1}\right) \frac{\sum^{n'} (1/T_i)^2 - (1/n')\left[\sum^{n'} (1/T_i)\right]^2}{[\sum (1/T_i)]^2}, \quad (13)$$

and

$$v_{(z/t)(1/t)} = \frac{s_{(z/t)(1/t)}}{\bar{T}^2[\sum (Z_i/T_i) \sum (1/T_i)]/n'^2}$$

$$= \left(\frac{n'^2}{n'-1}\right)$$

$$\cdot \frac{\sum^{n'} [(Z_i/T_i) \cdot (1/T_i)] - (1/n')\left[\sum^{n'} (Z_i/T_i)\right]\left[\sum^{n'} (1/T_i)\right]}{\sum (Z_i/T_i) \sum (1/T_i)}.$$

Mean and Variance Estimators for Fishing Effort per Angler

When fishing effort per angler is itself the variable of interest, a bias-corrected estimate of its mean value can be computed as

$$T/\hat{N} = \frac{T}{(T/n') \sum (1/T_i)} = \frac{n'}{\sum (1/T_i)}; \quad (14)$$

$\hat{N}$ is estimated according to equation (5). The sample variance of $T/\hat{N}$ is

$$\widehat{\text{var}}(T/\hat{N}) = \left\{\frac{n'}{[\sum (1/T_i)]^2}\right\} s^2_{1/t},$$

which is a special case of equation (10) for which $s^2_{t/t} = 0$, $s_{(t/t)(1/t)} = 0$, and $s^2_{1/t}$ is defined by equation (11).

The relative variance associated with equation (14) can be estimated by

$$\text{rel } \widehat{\text{var}}(T/\hat{N}) = \frac{1}{n'} v^2_{1/t}$$

$$= \frac{n'}{n'-1} \left\{\frac{\sum^{n'} (1/T_i)^2}{[\sum (1/T_i)]^2} - \frac{1}{n'}\right\}; \quad (15)$$

$v^2_{1/t}$ is defined by equation (13). The estimates produced by equation (15) generally will fall in the range (0, +1) for any reasonable sample size n', because

$$\sum^{n'} (1/T_i)^2 < \left[\sum^{n'} (1/T_i)\right]^2.$$

Thus the application of equation (14) to intercept data produces bias-corrected (consistent) estimates of mean fishing effort per angler that are characterized by relatively high precision.

A Case Study

This case study focuses on two surveys: the Marine Recreational Fishery Statistics Survey and the Bay Area Sportfish Economic Survey.

The Marine Recreational Fishery Statistics Survey (MRFSS) is an annual survey of saltwater anglers that has been sponsored by the National Marine Fisheries Service since 1979. Its major purpose is to estimate catch and effort of marine anglers on a state-by-state basis. The MRFSS comprises telephone and on-site sampling components.

- MRFSS—TEL is a random telephone canvass of the general population of coastal counties. Its purpose is to determine (among other things) the proportions of households with at least one person who has gone saltwater fishing in the previous 12 months and in the previous 2 months, the average number of such 12-month and 2-month anglers per angling household, and selected details of each trip made by each angler in the 2 months preceding the telephone contact. The telephone survey is repeated with a new sample every 2 months throughout the year. Results are expanded to estimate aggregate fishing effort by mode and area during each 2-month survey wave.

- MRFSS—INT is an on-site creel survey conducted throughout the year at four mutually exclusive fishing modes: (1) beaches and banks, (2) piers and other constructions, (3) party and charter boats, and (4) private and rental boats. The main purpose of this creel survey is to determine the number, weight, and species composition of fish caught in different modes, areas, and times of year. Estimates of catch per unit effort are combined with estimates of fishing effort from the MRFSS—TEL to estimate aggregate catch.

In 1985–1986, the Southwest Fisheries Center of the National Marine Fisheries Service sponsored the Bay Area Sportfish Economic Survey (BASES). This survey sampled marine anglers residing in the 19 coastal counties of central and northern California for information about fishing expenditures and demographics as well as on participation.

The BASES survey was conducted as a mail follow-up to the central–northern California portion of the nationwide MRFSS—TEL (hereafter referred to as MRFSS—TEL*). Specifically, 12-month anglers in MRFSS—TEL* who agreed to answer additional questions were mailed a BASES questionnaire. This solicitation was repeated over seven 2-month survey waves, beginning with July–August 1985 and ending with July–August 1986. Of the 4,031 anglers identified in the MRFSS—TEL* over the BASES survey period, 3,184 agreed to fill out the mail questionnaire and 1,543 actually completed and returned it.

Because of the length of the BASES questionnaire, it would not have been feasible to collect BASES data at on-site interviews. However, one option considered during the survey design phase was to conduct BASES as a mail follow-up to the central–northern California portion of MRFSS—INT; given the large sample size of MRFSS—INT, this would have greatly expanded the number of potential BASES respondents at relatively low cost. However, a major concern (and a deciding factor in the decision to use MRFSS—TEL* for initial respondent identification) was that on-site intercept techniques tend to generate samples heavily biased toward avid anglers.

The following sections compare bias-corrected estimates of the mean number of trips per angler with arithmetic mean values computed from the BASES and MRFSS—INT data. They describe the relationship between angler avidity and various components of economic value. Finally, they provide a numerical example to illustrate the potential effect of the avidity bias on estimates of annual economic value per angler.[2]

Effect of the Avidity Bias on Estimates of Fishing Effort

Ordinarily, all anglers contacted in MRFSS—INT, regardless of state or county of origin, are eligible for inclusion in the survey. In contrast, potential BASES respondents were limited to anglers residing in 19 designated counties. To ensure comparability of the two samples, all analysis of MRFSS—INT in this paper is limited to respondents who were interviewed at fishing sites in central and northern California over the BASES survey period and who reside in the counties from which the BASES sample was drawn. This subset of MRFSS—INT respondents is hereafter referred to as MRFSS—INT*.

The level of fishing effort reported by a sample of anglers can be affected not only by avidity bias but by respondents' proximity to fishing opportunities and by mode preferences. To isolate the latter effects from the effect of the avidity bias, the BASES and MRFSS—INT* samples were divided into subsamples.

Eighteen of the 19 counties of residence covered by BASES were grouped into five areas: inland, east bay, north coast, central coast, and south coast.[3] Each area is a group of contiguous counties with similar access to fishing opportunities. Specifically, north and south coast anglers have ready access to ocean fishing. Central coast anglers are close to both the ocean and San Francisco Bay, whereas east bay anglers have good access to the bay but not to the ocean. Inland anglers generally have poor access to all marine fishing opportunities.

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[2] The issue of length-of-stay bias is not addressed in this paper. For the most part, MRFSS—INT is an access point rather than a roving creel survey, so the probability of being sampled is related to the frequency of participation rather than length of stay.

[3] The counties included in each area were as follows: inland—Sacramento, San Joaquin, Yolo; east bay—Alameda, Contra Costa, Napa, Santa Clara, Solano; north coast—Del Norte, Humboldt, Mendocino, Trinity; central coast—Marin, San Francisco, San Mateo, Sonoma; south coast—Monterey, Santa Cruz. San Benito county was also included in the BASES survey but not covered in this analysis. It was deemed too far south to be included with the east bay counties and too far inland to be included with the south coast counties.

TABLE 1.—Comparison of bias-corrected, BASES, and MRFSS—INT* statistics on annual number of trips per angler, by fishing mode and area of residence.[a]

Area of residence and data source	Beach			Pier			Party boat			Private boat		
	Mean	CV	*N*	Mean	CV	*N*	Mean	CV	*N*	Mean	CV	*N*
Inland												
Bias-corrected	2.41	0.08	113	2.03	0.07	149	1.36	0.03	215	2.86	0.11	126
BASES	6.46	1.15	35	6.59	2.90	22	3.48	1.31	46	12.13	1.37	60
MRFSS—INT*	7.90	1.38	113	9.81	3.52	149	4.22	3.19	215	12.83	1.54	126
East bay												
Bias-corrected	3.87	0.05	690	3.59	0.04	863	1.95	0.03	615	4.20	0.04	1,316
BASES	8.98	1.45	111	11.05	1.92	55	3.59	1.53	145	12.25	1.65	199
MRFSS—INT*	23.67	1.69	690	21.99	1.67	863	9.04	1.93	615	19.77	1.15	1,316
North coast												
Bias-corrected	4.00	0.06	507	4.20	0.05	885	1.31	0.10	21	4.59	0.06	535
BASES	9.64	0.98	25	6.00	0.87	11	2.97	0.86	34	16.24	1.86	46
MRFSS—INT*	27.83	1.69	507	30.87	1.65	885	2.76	1.53	21	20.89	1.22	535
Central coast												
Bias-corrected	4.53	0.08	379	3.64	0.05	555	2.01	0.05	241	4.02	0.06	588
BASES	9.79	1.17	75	8.17	1.20	41	4.92	1.99	87	9.44	1.04	134
MRFSS—INT*	45.33	1.65	379	26.67	1.87	555	10.17	2.49	241	29.11	1.72	588
South coast												
Bias-corrected	5.05	0.08	342	4.81	0.09	258	1.73	0.06	157	4.46	0.08	312
BASES	18.35	1.58	26	5.68	1.02	16	4.03	0.95	35	10.53	1.46	47
MRFSS—INT*	38.69	1.58	342	39.42	1.65	258	14.18	3.08	157	24.92	1.71	312
All areas												
Bias-corrected	4.14	0.03	2,031	3.83	0.02	2,710	1.82	0.02	1,249	4.21	0.03	2,877
BASES	9.84	1.43	282	8.52	1.70	147	3.87	1.66	352	11.68	1.56	502
MRFSS—INT*	30.40	1.76	2,031	26.84	1.78	2,710	8.97	2.62	1,249	22.14	1.50	2,877

[a] Bias-corrected estimates of mean and coefficient of variation (CV) were computed according to equation (14) and the square root of equation (15), respectively.

Both BASES and MRFSS—INT* respondents were classified according to their "predominant" mode of fishing. For the BASES respondents, who provided detailed information (including mode) for the three most recent fishing trips made in the previous year, this was considered the mode of the last trip.[4] For the MRFSS—INT* respondents, who provided the number of fishing trips made in the previous year but did not identify them by mode, this was considered the mode of intercept.[5]

For each area–mode combination, I obtained an unbiased estimate of mean fishing effort per angler by applying equation (14) to the appropriate MRFSS—INT* subsample. I computed the associated coefficient of variation by taking the square root of equation (15). These statistics, as well as the arithmetic means and coefficients of variation for the corresponding BASES and MRFSS—INT* samples, are shown in Table 1.

The small BASES sample sizes associated with some area–mode combinations may make the reliability of some tabulated statistics questionable. The results, however, consistently indicate overrepresentation of avid anglers in the BASES and MRFSS—INT* samples relative to the angling population as a whole.[6] Another notable result is that the coefficients of variation associated with the bias-corrected estimates are uniformly close to 0, which reflects a substantial gain in precision over the BASES and MRFSS—INT* estimates.

The bias in the BASES sample can be attributed to a systematic pattern of nonresponse to the mail questionnaire. According to Thomson and Huppert (1987), anglers contacted in the MRFSS—TEL* who fished frequently in the previous 2 months were much more likely to complete the BASES mail questionnaire than those who fished infrequently or not at all during those 2 months. Two-month avidity was considerably higher for the BASES respondents than for the original telephone sample from which they were drawn, but it was impossible to determine whether nonresponse to the BASES questionnaire was related to 12-month avidity, because information on the number of trips made in the past 12 months is not collected in the MRFSS—TEL.[7] The differences between the unbiased and BASES estimates of mean fishing effort reported in Table 1, however, suggest the presence of a 12-month as well as a 2-month bias in the BASES sample associated with nonresponse to the mail questionnaire.

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[4] For 89% of the BASES sample, at least half of the three most recent trips were made in the mode of the most recent trip.

[5] MRFSS—INT defines a trip as a fishing day. The BASES definition of a trip includes both single- and multiple-day fishing excursions. To make the samples comparable, I excluded multiple-day trips from the analysis of the BASES data. Only 6% of the three most recent trips reported by BASES respondents were multiple-day trips.

[6] Table 1 also points up differences in avidity among modes and areas. For instance, inland residents, whose access to marine fishing opportunities is most limited, fish less frequently than other anglers in all modes. Also, party-boat anglers tend to fish less frequently than anglers associated with other modes. The relatively high costs associated with party-boat trips may limit participation to some extent. Supply may be a limiting factor as well, particularly in the north coast area, where party-boat vessels only operate seasonally.

The differences between the bias-corrected and MRFSS—INT* estimates are even more pronounced, which suggests that failure to correct for avidity bias in the MRFSS—INT* can result in gross overestimates of fishing effort per angler. The differences also suggest that the BASES sample of mail respondents would have been even more biased toward avid anglers if it had been collected as an add-on to MRFSS—INT* rather than to MRFSS—TEL*.

Effect of the Avidity Bias on Estimates of Economic Value

The economic value of fishing comprises two components: expenditures related to fishing, and the maximum amount over and above actual expenditures that the angler is willing to pay to participate in the activity. The sum of the two components is referred to as the gross benefit associated with fishing; the latter component is referred to as net benefit or consumer surplus.

Estimates of economic value are affected by the avidity bias only to the extent that they are correlated with angler avidity. This section describes the relationship of avidity to annual trip-related expenditures, annual fishing-gear expenditures, and annual consumer surplus.

Annual trip-related expenditures.—The BASES questionnaire does not directly ask for information on annual trip-related expenditures. Instead, it asks respondents to describe expenditures for each of their three most recent trips in each of the following categories: (1) tackle (lures, sinkers, lines, rental equipment, licenses, and fish cleaning), (2) boat fees (for party-boat trips), (3) boat fuel (for private boat trips), and (4) amenities (food, beverages, lodging).

To determine whether expenditures per trip were related to avidity, I divided the trip data into four subsamples, one for each trip mode For each trip expenditure category within each of the four modes, I used regression analysis to determine the effect of fishing avidity on the level of spending. I was unable to find a statistically significant relationship for any of the expenditure categories in the four modes. Costs per trip were invariant with respect to avidity, so annual trip-related expenditures per angler can be expected to be proportional to the frequency of participation.

Annual gear expenditures.—Another category of expenditures covered by the BASES survey was annual purchase and repair of saltwater fishing gear and equipment (excluding boats, motors, trailers, and boat-related equipment). To determine the effect of avidity on annual gear expenditures, I divided the BASES sample of anglers into four different subsamples, each consisting of respondents sharing the same predominant mode (the mode of the most recent fishing trip). The regression results associated with the best fitting functional form for each subsample are reported in Table 2.

For each predominant mode, the relationship between annual gear expenditures and avidity was quadratic, with gear expenditures first increasing and then declining as avidity increased. Up to some point, more frequent participation implied greater investment in equipment and therefore higher expenditures. Beyond that point, however, anglers appeared to have accumulated sufficient equipment and their expenditures declined.

Annual consumer surplus.—Three standard assumptions in demand theory are (1) the satisfaction individuals derive from a good, as well as the maximum amount that they are willing to pay for it, declines with each additional unit consumed per unit time; (2) individuals consume additional units so long as their willingness to pay is greater than or equal to the price of the good; and (3) willingness to pay is equal to price for the final unit consumed per unit time. Because individuals generally are required to pay the same unit price regardless of the quantity consumed, they derive

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[7] If annual participation data were collected in MRFSS—TEL, I would expect to find no statistically significant differences between the arithmetic mean of this variable from MRFSS—TEL and the bias-corrected mean from MRFSS—INT.

TABLE 2.—Results (coefficients) of regression analysis that describe the effect of angler avidity on annual gear expenditures (*t*-values in parentheses).[a]

Explanatory variables[b]	Fishing mode Beach	 Pier	 Party boat	 Private boat
T	10.994	4.207	18.520	14.452
	(9.779)	(5.286)	(7.157)	(6.239)
T^2	−0.162	−0.035	−0.270	−0.071
	(−5.021)	(−4.065)	(−4.999)	(−4.885)
INCOMEHI		40.708	48.515	136.092
		(2.921)	(2.531)	(2.817)
BOATOWNR				93.167
				(2.227)
Adjusted r^2	0.39	0.26	0.22	0.26
Sample size	251	131	314	447

[a] Annual gear expenditures cover purchase and repair of saltwater fishing gear and equipment (excluding boats, motors, trailers, and boat-related equipment).

[b] T is the number of fishing trips made in the previous 12 months. INCOMEHI = 1 if annual household income > \$50,000, 0 otherwise. BOATOWNR = 1 if angler owns a boat that can be used for saltwater fishing, 0 otherwise.

benefits over and above actual expenditures for all of the units consumed before the last one. This additional benefit is known as consumer surplus.

One commonly used method for measuring consumer surplus involves estimation of a demand or travel cost model $T = f(P, Z)$ that relates the number of trips (T) made per unit time with the travel cost or price per trip (P) and other relevant variables (Z). Consumer surplus is measured as the area under the demand curve above price. The general formula for consumer surplus is

$$\mathrm{CS} = \int_{P^*}^{P^{**}} f(P, Z)\, dP\,;$$

P^* is the actual price paid by the angler and P^{**} is the "choke price" that would cause the angler to stop fishing altogether.

I estimated a separate travel cost model for four subsets of the BASES sample, with each subset consisting of respondents sharing the same predominant mode (the mode of the most recent fishing trip). For the beach, pier, and party-boat modes, the final model specification took the form

$$T_i = \beta_0 + \beta_1 P_i + \beta_2 P_i^2 + \beta_3 \mathrm{ABIL}_i + u_i\,; \qquad (16)$$

T_i is the number of fishing trips made in the previous 12 months by angler i, P_i is the price or travel cost per trip incurred by angler i, ABIL_i is a dummy variable denoting angler i's self-described fishing ability (0 if fishing ability is average or less, 1 if fishing ability is greater than average), and u_i is a random error term. The quadratic term in P_i was excluded from the model specification for the private boat mode, because the coefficient β_2 was not statistically significant.

I computed P_i as the sum of mileage and time costs per trip. I estimated mileage costs by the number of round-trip highway miles between the angler's ZIP code of residence and the site of the most recent fishing trip, multiplied by vehicle operating costs of \$0.20/mi. I estimated travel time by assuming that travel distance was covered at a rate of 40 mph. Following Cesario (1976), I estimated the opportunity cost of time by multiplying travel time by one-third of the angler's reported wage rate.

The sample used to estimate the demand function was truncated (limited to anglers who made at least one fishing trip over the previous year), so I used a maximum-likelihood procedure based on a truncated normal distribution to obtain consistent parameter estimates (Maddala 1983). The empirical results appear in Table 3.

For the beach, pier, and party-boat equations, the change in the number of trips taken associated with a change in price was measured by $\delta T/\delta P = \beta_1 + 2\beta_2$; for the private boat equation, it was $\delta T/\delta P = \beta_1$. The parameter estimates in Table 3 produced the expected negative relationship between T and P for all four fishing modes. The estimated coefficient of ABIL was positive and significant for all four modes, which suggested that skilled anglers tended to fish more frequently.

Equation (16) can be used to compute annual consumer surplus,

$$\begin{aligned}\mathrm{CS}_i &= \int_{P_i^*}^{P_i^{**}} (\beta_0 + \beta_1 P_i + \beta_2 P_i^2 + \beta_3 \mathrm{ABIL}_i + u_i)\, dP_i \\ &= \left.\frac{(\beta_0 + \beta_1 P_i + \beta_2 P_i^2 + \beta_3 \mathrm{ABIL}_i + u_i)}{2(\beta_1 + 2\beta_2)}\right|_{P_i^*}^{P_i^{**}} \\ &= -\frac{T_i^2}{2(\beta_1 + 2\beta_2)}\,, \qquad (17)\end{aligned}$$

for anglers whose predominant mode is beach, pier, or party boat. For anglers whose predominant mode is private boat (for which $\beta_2 = 0$), consumer surplus takes the form

$$\mathrm{CS}_i = -\frac{T_i^2}{2\beta_1}\,. \qquad (18)$$

TABLE 3.—Results of travel cost model estimation (asymptotic *t*-values in parentheses).

Independent variables[a]	Fishing mode Beach	 Pier	 Party boat	 Private boat
CONSTANT			3.446 (4.862)	
P	−0.767 (−4.727)	−3.206 (−12.050)	−0.694E−1 (−2.234)	−0.498 (−25.091)
P^2	0.506E−2 (3.948)	0.197E−1 (7.024)	−0.647E−3 (−3.519)	
ABIL	19.977 (10.516)	16.332 (2.254)	5.557 (6.541)	17.867 (8.042)
Maximum log likelihood	−688.90	−413.12	−801.65	−1,377.60
Restricted log likelihood	−807.67	−510.47	−936.99	−1,594.20
Chi-square	237.54	194.70	270.68	433.20
Sample size	209	122	291	373

[a] *P* includes mileage costs and opportunity cost of travel time. ABIL is a dummy variable for the angler's self-described fishing ability (0 = intermediate or lesser ability, 1 = greater than intermediate ability).

Because the square of T_i appears in the numerator of equations (17) and (18), consumer surplus estimates derived from these equations are likely to be highly sensitive to the presence of avidity bias in an on-site intercept survey.

In general, the effect of the avidity bias on estimates of consumer surplus depends not only on the extent of the bias but on the functional form of the travel cost model. For instance, Bockstael et al. (no date) showed consumer surplus per angler associated with the commonly used semilog functional form

$$\log_e(T_i) = \beta_0 + \beta_1 P_i + \beta_2 Z_i + u_i$$

to be

$$\mathrm{CS}_i = -\frac{T_i}{\beta_1}. \tag{19}$$

Use of this semilog model produces consumer surplus estimates that are less sensitive to the avidity bias of an intercept sample than is the linear model specified in equation (16). This is due to the appearance of T_i rather than T_i^2 in the numerator of equation (19). However, attempts to estimate a semilog version of the travel cost model with the BASES data produced uniformly poor results for all modes.

Case Study Results

Table 4 provides a numerical example that describes the effects of the avidity bias in the MRFSS—INT* survey and the nonresponse bias in the BASES survey on various components of economic value. The data focus on east bay anglers, who make up approximately 46% of the angling population residing in the coastal counties covered by the BASES survey (Thomson and Huppert 1987).

The analysis underlying Table 4 is based on the assumption that the relationship of fishing avidity to annual gear expenditures (as described in Table 2) and to annual consumer surplus (as described in equations 17 and 18) applies to the angling population as a whole and to the MRFSS—INT* and BASES samples. Proceeding from this assumption, I estimated the following value components.

Annual Trip-Related Expenditures

I computed annual trip-related expenditures by multiplying mean cost per trip (as described in the following paragraphs) by the bias-corrected, BASES, and MRFSS—INT* estimates of mean number of trips per angler (from Table 1). The categories of cost included here are travel, tackle, party-boat fees, boat fuel, and amenities.

The same estimates of travel cost per trip that were used to estimate the travel cost model in Table 3 also were used for this numerical example. This includes (1) mileage costs, with travel distance valued at $0.20/mi, and (2) the opportunity cost of time, with travel time valued at one-third the angler's wage rate. By dividing the east bay residents in the BASES sample according to the predominant mode of each respondent, I computed mean travel cost per trip for each mode. I applied these same estimates to the east bay residents in MRFSS—INT*. This is a reasonable assumption for the mileage component, because all east bay residents are roughly equi-

TABLE 4.—Comparison of estimates of annual economic value per angler (corrected for avidity bias) with BASES and MRFSS—INT* estimates, for east bay residents.[a]

Fishing mode and quantity	Bias corrected	BASES mail survey	MRFSS—INT*
Beach			
Number of trips/year	3.87	8.98	23.67
Mean cost/trip			
Travel	$ 19.37	$ 19.37	$ 19.37
Tackle	$ 9.07	$ 9.07	$ 9.07
Amenities	$ 9.76	$ 9.76	$ 9.76
Total	$ 38.20	$ 38.20	$ 38.20
Annual trip-related costs	$147.83	$ 343.04	$ 904.19
Annual consumer surplus	$ 60.47	$ 164.16	$1,424.67
Annual gear expenditures	$ 27.69	$ 71.36	$ 83.22
Annual economic value	$235.99	$ 578.56	$2,412.08
Pier			
Number of trips/year	3.59	11.05	21.99
Mean cost/trip			
Travel	$ 13.76	$ 13.76	$ 13.76
Tackle	$ 9.19	$ 9.19	$ 9.19
Amenities	$ 10.18	$ 10.18	$ 10.18
Total	$ 33.13	$ 33.13	$ 33.13
Annual trip-related costs	$118.94	$ 366.09	$ 728.53
Annual consumer surplus	$ 12.48	$ 89.28	$ 288.52
Annual gear expenditures	$ 22.13	$ 53.63	$ 53.44
Annual economic value	$153.55	$ 509.00	$1,070.49
Party boat			
Number of trips/year	1.95	3.59	9.04
Mean cost/trip			
Travel	$ 12.69	$ 12.69	$ 12.69
Tackle	$ 15.39	$ 15.39	$ 15.39
Partyboat fees	$ 31.37	$ 31.37	$ 31.37
Amenities	$ 12.64	$ 12.64	$ 12.64
Total	$ 72.09	$ 72.09	$ 72.09
Annual trip-related costs	$140.58	$ 258.80	$ 651.69
Annual consumer surplus	$124.91	$ 303.94	$2,739.84
Annual gear expenditures	$ 44.34	$ 45.58	$ 95.48
Annual economic value	$309.83	$ 608.32	$3,487.01
Private boat			
Number of trips/year	4.20	12.25	19.77
Mean cost/trip			
Travel	$ 20.54	$ 20.54	$ 20.54
Tackle	$ 13.70	$ 13.70	$ 13.70
Boat fuel	$ 15.74	$ 15.74	$ 15.74
Amenities	$ 9.16	$ 9.16	$ 9.16
Total	$ 59.14	$ 59.14	$ 59.14
Annual trip-related costs	$248.39	$ 724.47	$1,169.20
Annual consumer surplus	$ 83.37	$ 558.23	$ 908.90
Annual gear expenditures	$148.80	$ 239.90	$ 315.47
Annual economic value	$480.56	$1,522.60	$2,393.57

[a] Number of trips per year taken from Table 1 for east bay residents. Travel costs were computed from data provided by east bay residents in the BASES sample; they include mileage costs (valued at $0.20/mi) and the opportunity cost of travel time (valued at one-third the angler's wage rate). Expenditures per trip on tackle, boat fees (for party-boat anglers), boat fuel (for private boat anglers), and amenities (food, beverage, and lodging) were obtained by averaging values reported for the three most recent trips by east bay residents in the BASES sample. Annual consumer surplus for the BASES and MRFSS—INT* samples were computed from equations (17) and (18) and the parameter estimates in Table 3. Annual gear expenditures for east bay residents in the BASES sample were computed by taking sample average. Annual gear expenditures for the MRFSS—INT* sample were estimated from Table 2. Bias-corrected consumer surplus and gear expenditures were computed by weighting the MRFSS—INT* values according to the formula in equation (7).

distant from fishing opportunities. For the opportunity cost component, I assumed that the opportunity cost of travel time is not a function of avidity.

The BASES questionnaire asked respondents for information regarding expenditures on tackle, party-boat fees, boat fuel, and amenities for their three most recent fishing trips. I divided the trip data provided by east bay residents into four subsets that corresponded to the mode of the trip; then I obtained an average expenditure value for each combination of mode–expenditure category. The same per trip expenditures were assumed for the east bay residents in the MRFSS—INT* sample. This assumption appears reasonable because of the lack of any statistically significant relationship between per trip expenditures and avidity.

Annual Gear Expenditures

I divided the east bay residents in the BASES sample into four subsamples, each consisting of respondents who shared the same predominant mode (the mode of the most recent fishing trip). I computed average annual gear expenditures for each mode on the basis of actual figures reported by the respondents.

Information on gear expenditures was not collected from MRFSS—INT* respondents. Therefore, for each east bay resident i in the MRFSS—INT* sample, I estimated annual gear expenditures by evaluating the equation in Table 2 that corresponded to the angler's predominant mode (the mode of the intercepted trip) at T_i. I then averaged these estimated values for all respondents associated with each mode.

I computed the bias-corrected estimate of average annual gear expenditures associated with each mode by applying the formula in (7) to the estimated values for the east bay residents in the MRFSS—INT* sample.

Annual Consumer Surplus

I estimated consumer surplus for each east bay resident in the BASES sample on the basis of formula (17) or (18), depending on the predominant mode of the respondent and the parameter estimates in Table 3. The values reported in Table 4 are the sample averages that correspond to each mode. The same procedure was used for the MRFSS—INT* sample. The bias-corrected estimates were obtained by applying the formula in equation (7) to the consumer surplus estimates for the MRFSS—INT* sample.

Magnitude of Bias

The differences in annual trip costs among the three samples were proportional to the differences in mean avidity levels. The BASES estimates were 0.8–2.1 times larger and the MRFSS—INT* estimates were 3.6–5.1 times larger than the bias-corrected values.

The differences in average annual gear costs were of lesser magnitude, with BASES estimates 0–1.6 times larger and MRFSS—INT* estimates 1.1–2.0 times larger than the bias-corrected estimates.

The differences in average annual consumer surplus were sizeable. The BASES estimates were 1.4–6.2 times larger and the MRFSS—INT* estimates were 9.9–22.6 times larger than the bias-corrected estimates. As discussed previously, this result is due in part to the use of a functional specification for the travel cost model that is linear in parameters.

When all components of value were summed, the BASES estimates of total value were 1.0–2.3 times larger and the MRFSS—INT* estimates were 4.0–10.3 times larger than the bias-corrected estimates.

Conclusions and Recommendations

Although on-site intercepts can be a relatively inexpensive way to locate potential respondents for economic surveys, the resulting sample will be biased toward avid anglers. The bias may not equal the magnitude of the case study reported here; yet it must be considered whenever intercept surveys are used to collect economic information.

By taking into account the nonuniform selection probabilities associated with intercept surveys, it is possible to derive bias-corrected (consistent) and relatively precise estimates of mean number of trips per angler from intercept data. When the sample size is sufficiently large, it is possible also to obtain unbiased statistics for other variables correlated with angler avidity.

Some functional forms for the travel cost model (such as the linear-in-parameters model) yield estimates of consumer surplus that are more sensitive to avidity bias than others (e.g., the semilog model).

Avidity bias may be present among mail survey respondents drawn from a random sample of anglers (such as BASES). In this case, the bias is caused by nonresponse to the mail questionnaire rather than by the sample selection procedure.

Although I have only peripherally addressed the issue of nonresponse bias, I do not mean to minimize its importance.

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References

Bockstael, N. E., W. M. Hanemann, and I. E. Strand, Jr., editors. No date. Measuring the benefits of water quality improvements using recreation demand models. Benefit analysis using indirect or imputed market methods, volume 2. Prepared for U.S. Environmental Protection Agency, Contract CR-811043-01-0, Washington, D.C.

Cesario, F. J. 1976. Value of time in recreation benefit studies. Land Economics 52:32–41.

Cochran, W. G. 1977. Sampling techniques. Wiley, New York.

Jessen, R. J. 1978. Statistical survey techniques. Wiley, New York.

Maddala, G. S. 1983. Limited dependent and qualitative variables in econometrics. Cambridge University Press, Cambridge, UK.

Nowell, C., M. A. Evans, and L. McDonald. 1988. Length-biased sampling in contingent valuation studies. Land Economics 64:367–371.

Thomson, C. J., and D. D. Huppert. 1987. Results of the bay area sportfish economic study (BASES). NOAA (National Oceanic and Atmospheric Administration) Technical Memorandum NMFS (National Marine Fisheries Service) SWFC (Southwest Fisheries Center) 78, La Jolla, California.

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CRABS FROM THE MARIANA ARCHIPELAGO: *BOTHROMAIA GRIFFINI* NEW GENUS AND SPECIES (BRACHYURA: MAJIDAE), AND REMARKS ON *POUPINIA HIRSUTA* GUINOT (HOMOLOIDEA, POUPINIIDAE)

Austin B. Williams and Robert B. Moffitt

Abstract.—Deepwater trapping in the Mariana Archipelago, western North Pacific Ocean, included incidental catches of a spider crab and a homoloid crab with novel characteristics. *Bothromaia griffini,* new genus and species, family Majidae, subfamily Inachinae, represented by a male and female, seems most closely related to the genus *Pleistacantha* Miers, containing several species distributed in Indo-Pacific waters. The new species resembles members of this genus with respect to presence of pseudorostral horns, and shape of eyestalks, basal antennal article, epistome, third maxilliped, male sternites and pleopod 1, but differs from them in shape of pseudorostral horns, carapace, male pleopod, and in proportions of the ambulatory legs. Descriptions, illustrations, and comparative discussion are presented. Notes on the homoloid crab, *Poupinia hirsuta* Guinot, include locality data, measurements, remarks on distribution, and discussion of features distinguishing the families of Homoloidea, including a key for their identification.

During 1982–1984 field studies of the Resource Assessment Investigation of the Mariana Archipelago (RAIOMA) program in the western North Pacific Ocean, conducted by the National Marine Fisheries Service Southwest Fisheries Science Center Honolulu Laboratory, deepwater trapping operations concentrated on the pandalid shrimp species *Heterocarpus laevigatus* Bate, 1888 (see Polovina et al. 1985, Moffitt & Polovina 1987). Included in incidental trap catches was a female spider crab and a male homoloid crab with novel characteristics. Examination of additional preserved material from a 1971 trip to the same area yielded a male specimen of the spider crab that was collected in a shrimp trawl. The two spider crabs are herein described as a new genus and species of the family Majidae. The homoloid crab belongs to a species described from Raiätea, Society Islands, Polynesia, *Poupinia hirsuta* Guinot, 1991, that was placed in a new family Poupiniidae. Notes on the specimen reported here include locality data, measurements, discussion of structure and relationships, and a key to the homoloid families.

The specimens are deposited in the crustacean collection of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). Comparative studies were made using collections of the USNM, the Australian Museum, Sydney (AMS), Bernice P. Bishop Museum, Honolulu, Hawaii (BPBM), and the Queensland Museum, Brisbane, Australia (QM).

Family Majidae Samouelle, 1819
Subfamily Inachinae MacLeay, 1838
Bothromaia, new genus

Diagnosis.—Carapace pyriform, moderately broad, surface unevenly granular;

branchial regions swollen, deeply recessed urogastric region partly covered by projecting cardiac region and confluent anterolaterally with excavate cervical groove; conspicuous, slender spines on frontal, gastric, cardiac and branchial regions, and along anterolateral margins. Rostrum triangular, abruptly deflexed dorsally, ending in slender median spine; pseudorostral lobe near apex of antennular fossa distally ornamented with cluster of radiating spines. Supraorbital eave spinose, posterior margin of orbit open, allowing retraction of eyestalk. Eyestalks stout, small spine on corneal emargination. Basal antennular article broad, that of antenna long and not fused to front, both with ventral spines. Epistome broad. Merus of third maxilliped extended distally at distolateral corner, slightly narrower than ischium, merus and ischium spined ventrally. Cheliped of female (unknown in male) longer than carapace but only ⅔ length of first ambulatory leg. Ambulatory legs moderate in length, diminishing successively from first to last, somewhat flattened, setose, spiny, and granular on nearly all surfaces. First pleopod of male with shaft tapered, essentially straight except for distal section directed anterolaterally, subterminal aperture on mesial surface preceded by longitudinal tract of fine setae and succeeded by small spinelike process.

Type species.—*Bothromaia griffini* new species.

Etymology.—From the Greek, "bothros," trench, pit, hollow, and "maia," a kind of crab, with reference to the deep pit in the urogastric region. The gender is feminine.

Bothromaia griffini, new species

Figs. 1–4

Material.—Commonwealth of the Northern Mariana Islands: USNM 250884, holotype ♂, W of Saipan Island, 15°10.1′N, 145°39.9′E, 366–379 m, *Townsend Cromwell* cruise 53, sta 94, 30 Apr 1971, shrimp trawl (chelipeds missing, ambulatory legs separated from body).—250885, allotype ♀, Esmeralda Bank, 14°58.4′N, 145°15.8′E, 377 m, *Townsend Cromwell* cruise 82-02, sta 23 string 3, 23 Apr 1982, shrimp trap.

Measurements of carapace (mm).—Holotype ♂, overall length 33.3, fork length in midline 29, width to base of lateral spines 22, width including lateral spines (tips broken) 25.8; allotype ♀, same measurements 37.8, 36.7, 26.7, width including lateral spines 28.8.

Description.—Carapace pyriform, width about ⅔–¾ length, surface unevenly granular. Deeply recessed urogastric region confluent anterolaterally with excavate cervical groove.

Frontal region strongly depressed, triangular, ending in slender median (interantennular) spine directed anteriorly and slightly ventrad, tip slightly exceeding spine-tipped pseudorostral lobes at distolateral corner of each antennular fossa; pseudorostral lobes short (basal length 1.5 mm), blunt, bearing cluster of 4 radiating short spines apically; well developed spine below these near lateral margin of each antennular fossa flanked dorsally by smaller similar spine on lateral margin of pseudorostral lobe, and preceded by graduated series of spines on lateral margin of fossa, increasing to ventrolaterally projecting spine near its base.

Several spines on nearly semicircular supraorbital eave; margin bearing about 7 closely crowded small spines on anterior ⅓, much more scattered small spines on central and posterior ⅓; 3 much stronger submarginal spines (moderate anterior, very strong dorsal, smaller posterolateral); postorbital spine obscurely compound, but posterior margin of orbit open to allow retraction of eyestalk. Pair of strong epigastric spines posteromesial to pseudorostral lobes, pair of protogastric spines at anterior part of swollen gastric region; latter with 4 prominent spines at apices of rhombic array, anterior-most medial in middle of mesogastric region followed by 2 metagastrics projecting posterolaterally over right and left cervical

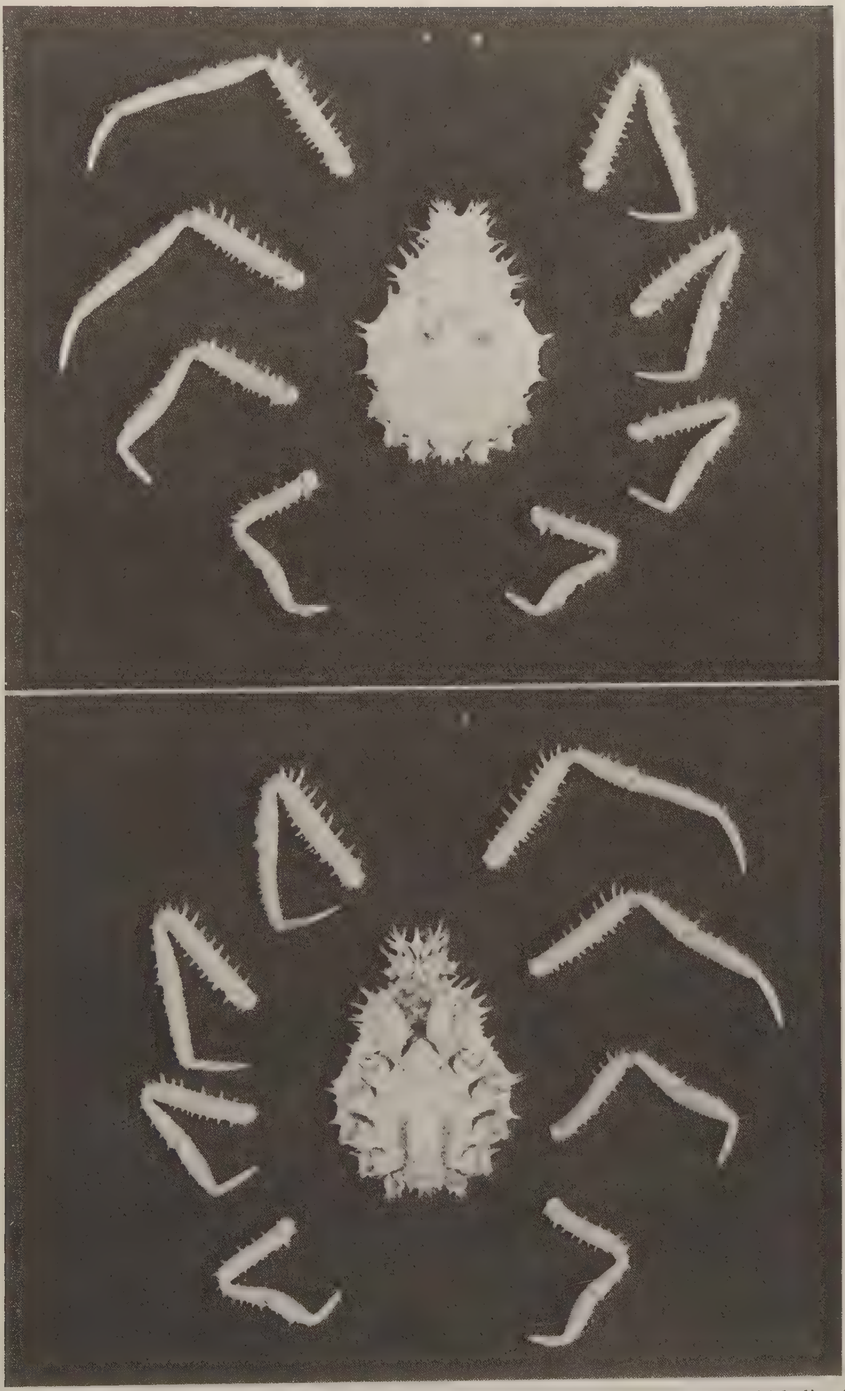

Fig. 1. *Bothromaia griffini,* new genus and species. Holotype ♂: upper, dorsal; lower, ventral (chelipeds missing, disarticulated legs arranged in order of succession).

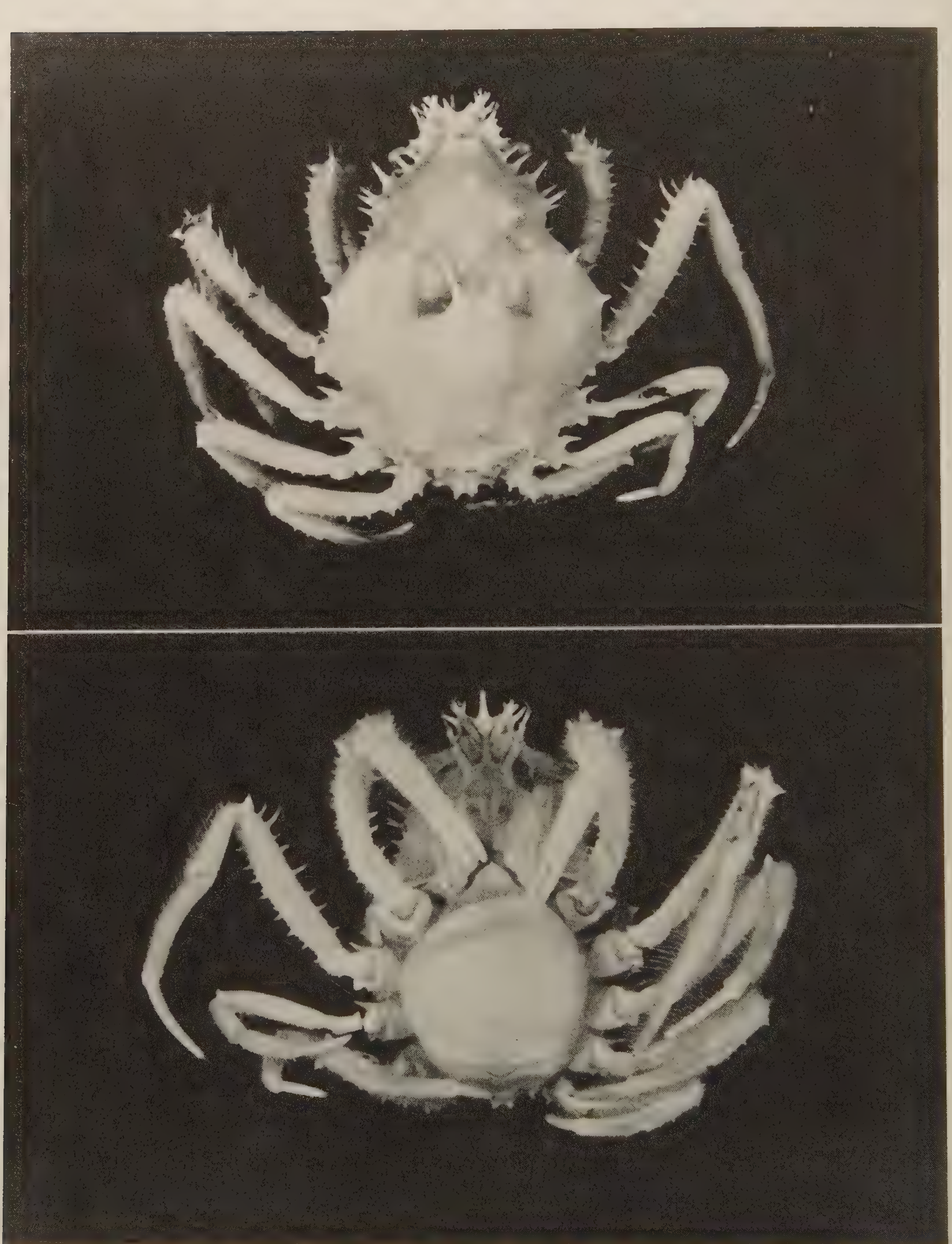

Fig. 2. *Bothromaia griffini*, new genus and species. Allotype ♀: upper, dorsal; lower, ventral.

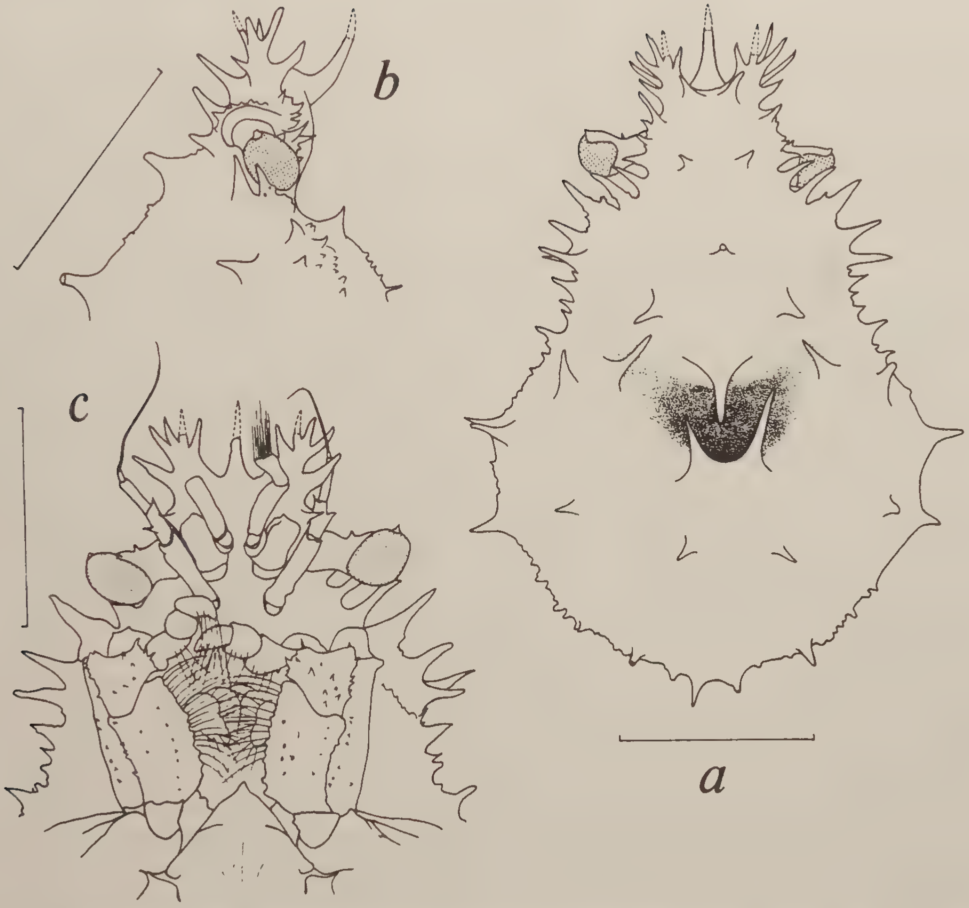

Fig. 3. *Bothromaia griffini*, new genus and species. Holotype ♂: a, carapace, dorsal; b, same, right lateral; c, cephalic region, ventral. Scales = 1 mm.

grooves, and posterior-most median extending posteriorly over recessed urogastric region. Cardiac region swollen and bearing 2 unequal pairs of spines; stronger anterior pair horizontally divergent from edge of regional extension over urogastric pit, shorter posterior pair near middle of region erect but laterally divergent. Intestinal region bearing pair of posteriorly projecting spines, stronger in male than in female. Each branchial region bearing 7 spines; large spine on anterior part of epibranchial region extending anteromesially over cervical groove, posterolateral to it another spine; mesobranchial region with dorsal spines at level of urogastric pit and cardiac region, and 2 others obliquely and lateroventrally in line with these respectively at perimeter of region; posterior-most spine near intestinal spines and well separated from preceding. Margin variably spiny in dorsal view, bearing 2 strong protogastric, 4 strong hepatic, and many smaller spines along branchial, posterolateral and intestinal sectors.

Eyestalks stout, bearing 2 small anterior spines on anterior surface of laterally extended eye, and 1 on corneal emargination, cornea twice width of stalk. Antennule with broad basal article spined ventrally. Basal antennal article slender, extending to basal

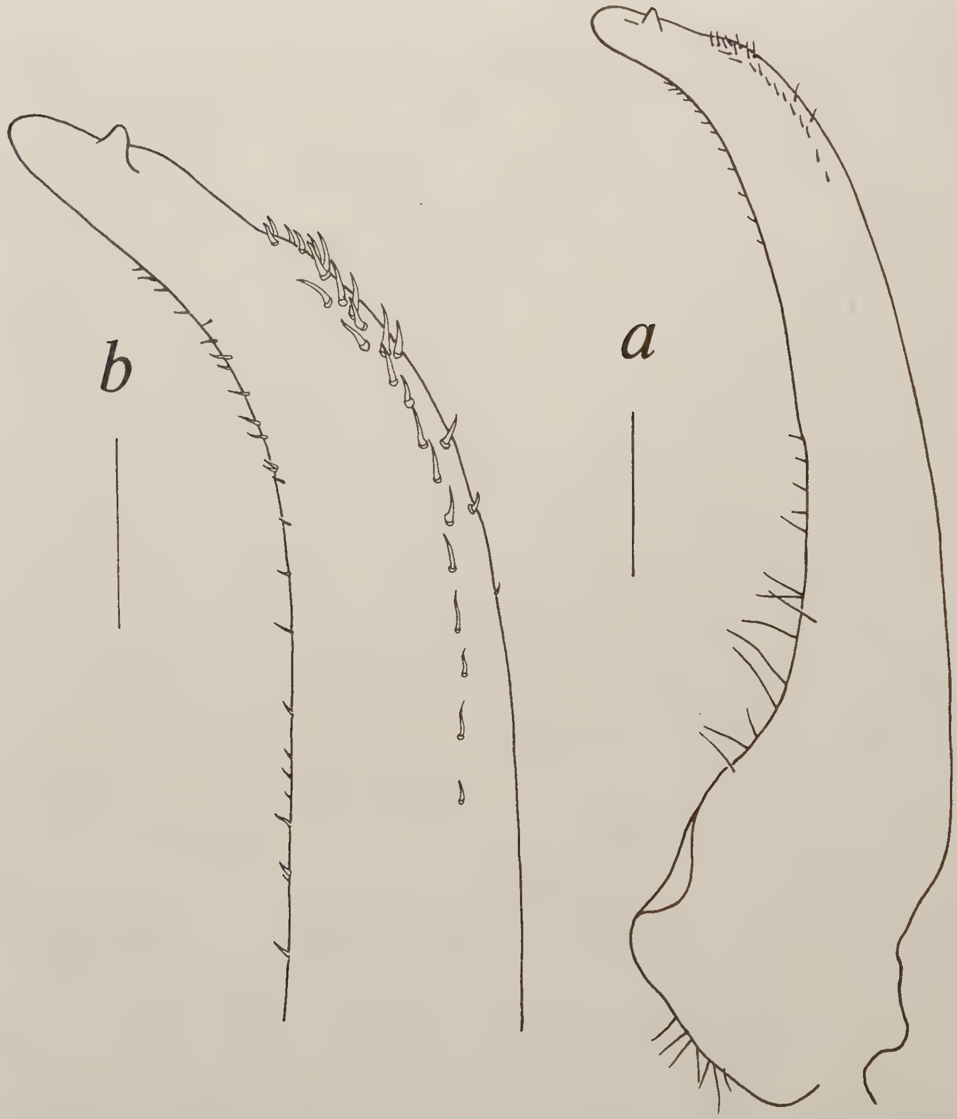

Fig. 4. *Bothromaia griffini* new genus and species. Holotype ♂ pleopod 1: a, abdominal view, b, magnified tip. Scales = 1 mm (a), 2.5 mm (b).

part of eyestalk, not fused to carapace, variably spined ventrally along mesial and lateral margins; middle and distal articles together reaching base of radiating spines on pseudorostral horn, middle article bearing ventral spine near middle of lateral margin and another spine variably developed at anteromesial corner.

Thoracic sternites of male bearing spines of varying sizes, most of them with seta originating near apex, and tendency to arrangement in submarginal row on each plate along radiating sutures; sternites of female not spinose, with raised thin lip where expanded 6th abdominal segment fits against them.

Abdomen of both sexes 6-segmented. That of female ampulliform in outline, with narrow neck lodged between coxae of fifth legs, narrowest point at suture between segments 1 and 2 (5.6 mm), widest point at approximate midlength of broadly cupped, operculiform telson (17.7 mm); midlength of successive segments 1–6 (3.5, 3.0, 2.2, 2.3, 2.6, 14.9 mm); exposed surface of segments 2–6 sparsely but unevenly setose, densest on 2–4, becoming quite sparse on distal ⅓ of telson; segment 1 bearing submarginal median tubercle anteriorly, submedian pair of spines succeeding it, and scattered granules; segment 2 with 2 pairs of submedian setose granules and remote setose granule laterally, segments 3–5 with same pattern, but submedian granules successively more suppressed and lateral granule successively more remote from midline; margin of telson narrowly reflected distally, less definitely so laterally, broad subterminal depression near shallow terminal concavity (asymmetrical on allotype), definite marginal notch at coxal level of first ambulatory leg, faint tract of median ornamentation on anterior half reminiscent of that on preceding segments.

Abdomen of male not broadened but more or less parallel sided except for sinuosities of individual segments, ornamentation as in female except spines and granules magnified; segment 3 broadest (5.5 mm); telson subrectangular, as wide as long (4.1 mm), bearing posterolateral notch, narrowly reflected terminal margin concave and broadly sunken, pattern of ornamentation in proximal half resembling that on preceding segments. First pleopod reaching level of suture between sternites adjacent to coxae of first and second ambulatory legs; shaft tapered, essentially straight except for distal section curved anterolaterad, subterminal aperture on mesial surface preceded by longitudinal tract of fine setae and succeeded by short spinelike process.

Third maxilliped with ischium bearing ventral row of moderate spines along ventrolateral rib, few spines and setose granules scattered over remainder of exposed surface, mesial margin heavily setose and armed with few small stout spines more numerous in proximal than distal half of length; exognath armed with ventral row of rather strong spines and lateral row of much smaller spines. Merus slightly narrower than ischium, extended distally into subtriangular lobe at distolateral corner, margin irregularly spined, ventral surface with 2 curved rows of spines originating near articulation with ischium, each terminating in slender marginal spine at either side of articulation with carpus. Flexed carpus-propodus-dactyl reaching halfway along length of ischium.

Cheliped of female (missing on male specimen) densely setose except on fingers, slightly longer than carapace but only ⅔ length of first ambulatory leg; merus bearing 1 mesiodorsal row of strong spines, tract of shorter spines dorsolaterally tending to arrangement in 2 obscure rows, 2 rows of spines ventrally and row of irregular spines mesioventrally, stoutest spines on each merocarpal condyle and longest spines distally on dorsolateral row; carpus bearing scattered spines tending to arrangement in obscure rows; palm slender, somewhat flattened, bearing scattered small spines strongest on extensor surface; fingers just over ½ length of palm, nearly straight, leaving only small proximal gap when closed, uniformly crenulate on cutting edges of left hand (cutter), teeth slightly stronger in basal half of right dactyl (crusher), fingers of crusher worn or broken at tips, perhaps slightly spooned.

Ambulatory legs setose, spiny, and granular on nearly all surfaces, moderate length diminishing successively from first to last, somewhat flattened; coxae strongly spined anterolaterally, a few spines on ventromesial surface; ambulatory leg 1 about 1.5 times carapace length (basis to tip of dactyl in male ~51 mm), merus with 3 terminal spines, 2 of these lateral at apex of triangular merocarpal condyles, rows of spines on dorsal and ventral margins, dorsal row strongest, posterior surface bearing many scattered spinules, anterior surface less ornamented; carpus and propodus bearing single row of small spines interspersed with longer spines on dorsal margin and scattered spines on posterior surface, crowded short spines and spiniform tubercles on ventral surface, many of them setose, anterior surface bearing few rows of setose granules; dactylus nearly as long as propodus and bearing many setae (sparse on anterior surface), but few small spines on prehensile surface, tip corneous. Succeeding ambulatory legs similar in ornamentation but successively shorter (length basis to tip of dactyl of male: leg 2, 50 mm; leg 3, 37 mm; leg 4, 33 mm).

Color.—A photograph of the allotype, taken against a light gray background at the time the specimen was collected, shows the overall color in dorsal view to be salmon; the frontal and gastric regions are darkest, but decorated by contrastingly lighter spines and tubercles of the same hue as the remainder of the body, including the legs; the cornea appears transparent.

Etymology.—The specific name honors D. J. G. Griffin, authority on majid crabs of the Pacific, and Director of the Australian Museum, Sydney.

Remarks.—*Bothromaia griffini* was studied with the aid of comparative reference to the discussions of *Pleistacantha* and *Cyrtomaia* species by Guinot (1985), Guinot & Richer de Forges (1982a, 1982b, 1985), Griffin & Tranter (1986), and Richer de Forges & Guinot (1988), and by comparisons with specimens in museum collections mentioned above. Depending on authority, *Pleistacantha* is regarded as containing 11 species and *Cyrtomaia* 24, all of which occur in deep waters of the Indo-Pacific.

Bothromaia seems closely allied to *Pleistacantha* Miers, 1879 in respect to: (1) shape of abruptly deflexed interantennular spine, although tip is bifurcate in some species of latter; (2) presence of armed pseudorostral horns; (3) well-developed eyestalks bearing expanded ovate cornea, with small spines on anterior surface of stalk and at corneal emargination; (4) basal antennal article slender, not fixed to front and bearing ventral spines; (5) epistome broad; (6) shape of ischium and merus of third maxilliped, (7) spined sternites on males; and (8) general conformation of male first pleopods.

Bothromaia differs from *Pleistacantha* in having: (1) short lobular pseudorostral horns, each bearing radiating cluster of spines at tip rather than being elongate horns armed with spines along length; (2) carapace rather inflated and relatively smooth on gastric and branchial regions bearing few conspicuous spines, and with deep urogastric pit confluent with excavated cervical groove overhung by extension of cardiac region as well as spines from it and neighboring regions, whereas that of *Pleistacantha,* somewhat depressed and lacking any evidence of urogastric pit, is densely armed with short spines; (3) ambulatory legs moderate in length, somewhat flattened, having rather stout meri, densely clothed with setae, spined, and fairly coarsely granulate, whereas those of *Pleistacantha* are long, cylindrical and spidery; (4) male first pleopods generally shaped as those in *Pleistacantha* species, but more obliquely angled terminal part, with aperture preceded by linear cluster of small setae, and process distal to aperture much shorter than in *Pleistacantha.*

Bothromaia griffini resembles species of *Cyrtomaia* Miers, 1886, in the generally rather smooth inflated carapace with its conspicuous slender spines, though not in the position and relative lengths of the spines, but many other features of *Cyrtomaia* species, such as shape of the carapace and its marginal spination, the rostrum, basal antennal article fused to front, eyes, and shape and dimension of legs, are quite different.

Superfamily Homoloidea de Haan, 1839

Family Poupiniidae Guinot, 1991

Poupinia hirsuta Guinot, 1991

Fig. 5

Material.—USNM 250886, ♂, Commonwealth of the Northern Mariana Islands,

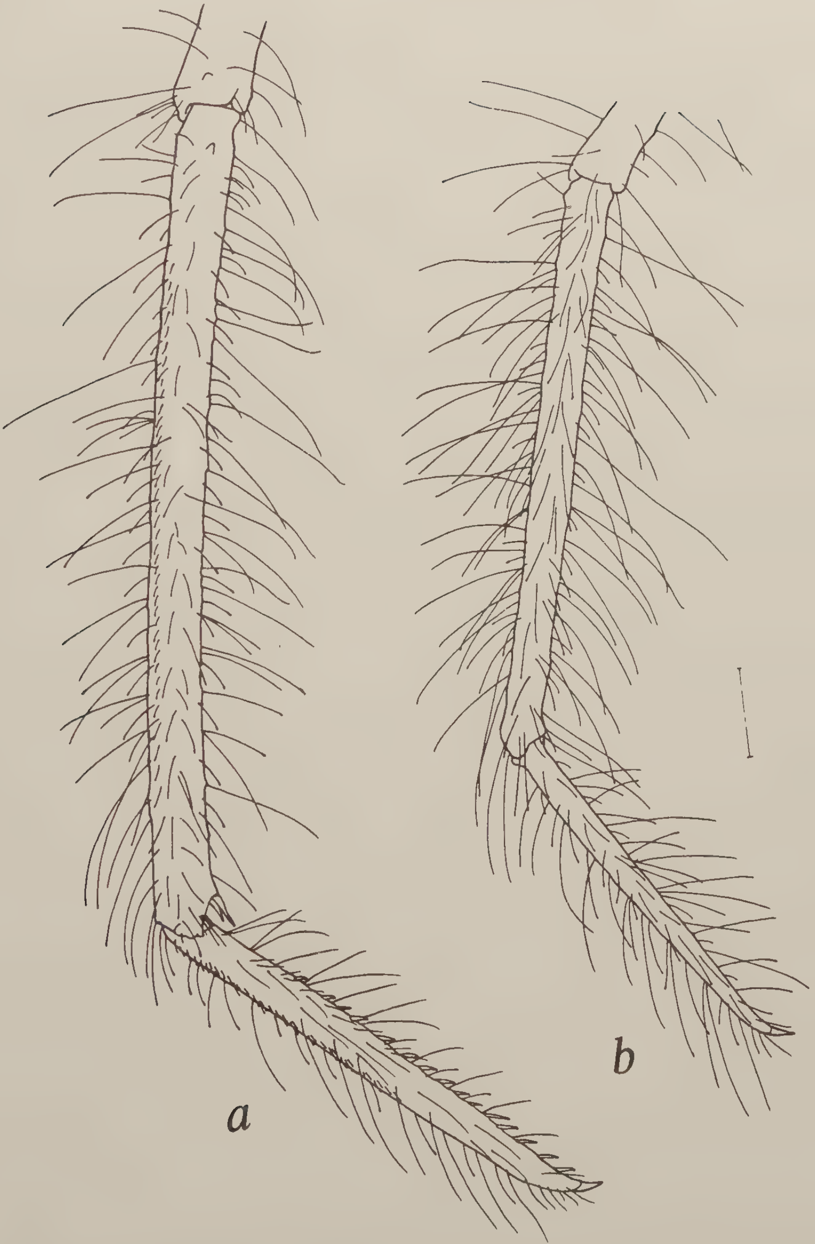

Fig. 5. *Poupinia hirsuta.* Male, semidiagrammatic dorsal view of distal articles on left fourth and fifth legs, ornamentation includes scattered setae with minutely spatulate tips: a, fourth leg with dactyl spined on flexor surface; b, fifth leg with spineless dactyl. Scale = 5 mm.

Table 1.—*Poupinia hirsuta* ♂, length in mm of articles in legs 1–5, right side.

Leg	Merus	Carpus	Propodus	Dactyl	Total
1	19	11	23	~11	53
2	33	28	29	18	108
3	43	23	35	22	123
4	48	20	41	25	135
5	44	16	32	22	114

Arakane Reef, 15°38.2′N, 142°46.3′E, 366–421 m, *Townsend Cromwell* cruise 83–05, sta 152, 16–17 Oct 1983, shrimp trap.

Measurements (mm).—Fork length of carapace in midline 33.4, maximum width 29.0; length legs, proximal end of merus to tip of dactyl, cheliped 41, 2nd leg 108, 3d leg 123, 4th leg 135, 5th leg 114.

Remarks.—The adult male specimen reported here is immediately recognizable as the striking homoloid species described by Guinot (1991) from baited trapping at similar depth in the Society Islands. The locality, however, is over 7000 km northwest of Raiatea, suggesting that the distribution of this species is widespread in the tropical southern and western Pacific.

Before establishment of the Poupiniidae, the Homoloidea were characterized as having the fifth legs dorsal in position, reduced, and subchelate or chelate. Discovery of *Poupinia hirsuta,* changes this definition. The new crab has fifth legs that originate in a dorsal position, but their length is intermediate beween that of the first, second, and third ambulatory legs (Table 1). The fifth legs are somewhat more slender than the preceding ambulatory legs, but not subcheliform, and they are less adapted for grasping than their antecedents, for the spineless dactyl does not close against spines on the flexor surface of the propodus, whereas each of the preceding ambulatories has its dactyl spined on the flexor surface, the proximal part of which closes between a pair of movable spines on the distal flexor surface of the propodus. The relatively unmodified and presumably primitive structure of this limb sets the new genus and species apart from all other members of the Homoloidea, which possess variously reduced and specialized subcheliform fifth legs.

The family Homolidae, often attributed to Henderson (1888) who gave the first comprehensive diagnosis, was actually authored by de Haan (1839) (International Commission on Zoological Nomenclature 1987). Alcock (1900, 1901) restricted the family Homolidae when he diagnosed the family Latreilliidae proposed by Stimpson (1858) (International Commission on Zoological Nomenclature 1987). Since then, students of these crabs have viewed the inclusiveness of these families in two ways (Williams 1982). Ihle (1913), Gordon (1950), Monod (1956), Balss (1957), Sakai (1965), and Serène & Lohavanijaya (1973), subsumed the Latreilliidae within the Homolidae. Griffin (1965), Glaessner (1969), Guinot (1979), Eldredge (1980), Guinot & Richer de Forges (1981), and Zarenkov & Khodkina (1981) did not concern themselves with this question, but Rathbun (1937), Wright & Collins (1972), Sakai (1976), Manning & Holthuis (1981), Williams (1982), Wicksten (1985), Melo (1990), and Guinot (1991) agreed with Alcock on distinctiveness of the two families. Collectively, these authors have recognized 38 living species of Homolidae and 9 species of Latreilliidae, although other undescribed species of the latter are known.

Wright & Collins (1972) observed that the essential characteristic distinguishing the Homolidae from the Latreilliidae is presence of the *linea homolica* in the former and its absence in the latter. They considered that other attributes such as number of gills and epipodites, relative lengths of basal and terminal articles of the eyestalks, and the more or less continuous range of carapace shapes, from rectangular (homolids) to acute-angled isosceles triangular (latreilliids), pale into insignificance when presence or absence of the *linea homolica* is considered. That seemingly essential dichotomy, represented among 25 recognized fossil species in 7 genera collectively summarized by Glaessner (1929, 1969), Wright & Collins (1972), Jenkins (1977), Bishop (1982, 1983, 1986), Takeda & Fujiyama (1983), and Förster & Stinnesbeck (1987), has existed since the early Upper Cretaceous, and was foretold in the Late Jurassic.

Although Wright & Collins (1972) characterized the Homolidae as having long slender legs, except for the reduced and dorsal fifth pair, fossil remains have either no legs preserved, or rare vestiges of them preserved. They described fossil *Homolopsis edwardsii* Bell, for example (paraphrasing, pp. 47–48), as having: chelipeds rather small; merus as long as carapace, longitudinally sulcate and slightly granulate; carpus cuboid; propodus as long as width of orbitofrontal margin; hands as long as wide, and oval in section; fingers slender and as long as or longer than hand. Ambulatory legs long and slender; meri angular in section, granulated and spinous on both borders. Nothing was said of the carpi, propodi, or dactyls, nor was reference made to characters of the fifth legs, but this species apparently offers no evidence to abridge the current family definition. Bishop (1983) figured his *Zygastrocarcinus griesi* with rather stout, coarsely granulated proximal articles on the chelipeds, and ambulatory legs 1, 2, and possibly 3, with rather stout, flattened, sulcate meri, but there is no evidence of the fifth pair of legs, although he did show them as reduced in dorsal position in a reconstruction drawing (fig. 2:901).

The significance of bilateral branchial count in the Homoloidea has received varied interpretation. Alcock (1900, 1901) perceived a clear distinction in branchial count between the Latreilliidae (8 gills and an epipodite on each of the 3 maxillipeds, although he did not analyze the count in *Latreillopsis* which he included in this family) and the Homolidae (14 gills and 6 epipodites, 1 on each of the 3 maxillipeds, the chelipeds, and ambulatory legs 1–2). Gordon (1950) found these differences in branchial count less clear-cut, for there is variation in branchial development among genera that Alcock grouped in the Homolidae, some having only 13 gills and 5 epipodites. Certain gills of some species tend to be reduced as well. *Latreillopsis* has only 10 gills and 4 epipodites, hence is intermediate in this respect between Alcock's standard for latreilliids and homolids. Griffin (1965) concurred that branchial count may be an unreliable character that needs further study. Still, latreilliids seem to be characterized by an essentially triangular carapace lacking the *linea homolica,* 8 gills and 3 epipodites, and fifth legs reduced and dorsal. Homolids have a subrectangular or ovoid carapace with *linea homolica,* 10 to usually 14 gills, 4 to usually 6 epipodites, and fifth legs reduced and dorsal.

The branchial formula of *Poupinia hirsuta* is incompletely known. Guinot (1991) observed epipodites on the first three legs, but possibly was reluctant to dissect rare perfect specimens to determine the full branchial formula, as are we. As a substitute for dissection, radiographs of our specimen indicate epipodites on maxilliped 3, the cheliped, and ambulatory legs 1–2. Faint outlines of gills seem to be evident on somites associated with maxilliped 3, the cheliped, and ambulatory legs 1–3, but the actual gill count cannot be ascertained from these images. The images indicate that the count may conform with that of the Homolidae rather than the Latreilliidae, or lie between these extremes.

Poupinia hirsuta, in the Poupiniidae, thus bridges these two groups in that it has an ovoid carapace with no *linea homolica,* epipodites on maxilliped 3, chelipeds, and ambulatory legs 1–2 (based on radiographs), seems to have a high gill count, and fifth legs normal in size, the most primitive condition, though originating in dorsal position. The suite of characters is set forth in the following:

Key to Families of Homoloidea

1. *Linea homolica* present .. Homolidae
- *Linea homolica* absent 2
2. Carapace ovate in dorsal outline, anterior part not extended into "neck" and prominent rostral horns; leg 5 normal, neither subchelate nor conspicuously diminished in length .... Poupiniidae
- Carapace sub-isosceles-triangular in dorsal outline, anterior part extended into "neck" and prominent divergent rostral horns; leg 5 conspicuously diminished in length, usually subchelate .... Latreilliidae

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Literature Cited

Alcock, A. 1900. Materials for a carcinological fauna of India. No. 5. The Brachyura Primigenia or Dromiacea.—Journal Asiatic Society of Bengal 68(2), No. 3:123–169.

———. 1901. Catalogue of the Indian decapod Crustacea in the collection of the Indian Museum. Part I. Brachyura. Fasciculus I. Introduction and Dromides or Dromiacea (Brachyura Primigenia). Calcutta, Printed by order of the Trustees of the Indian Museum, ix + 80 pp., plates A & 1–8.

Balss, H. 1957. Decapoda. VIII. Systematik. Dr. H. G. Bronn's Klassen und Ordnungen des Tierreichs. Bd. 5, Abt. 1, B. 7, Lf. 12:1505–1672, Leipzig, Akademische Verlagsgesellschaft, Geest & Portig K.-G.

Bate, C. S. 1888. Report on the Crustacea Macrura collected by H.M.S. Challenger during the years 1873–76.—Report on the Scientific Results of the Voyage of H.M.S. Challenger during the years 1873–76 . . . etc. Zoology 24, xc + 942 pp., 150 plates.

Bishop, G. A. 1982. *Homolopsis mendryki*: a new fossil crab (Crustacea, Decapoda) from the Late Cretaceous *Dakoticancer* Assemblage, Pierre Shale (Maastrichtian) of South Dakota.—Journal of Paleontology 56:221–225.

———. 1983. Two new species of crabs, *Notopocorystes (Eucorystes) eichhorni* and *Zygastrocarcinus griesi* (Decapoda: Brachyura) from the Bearpaw Shale (Campanian) of north-central Montana.—Journal of Paleontology 57:900–910.

———. 1986. A new crab, *Zygastrocarcinus cardsmithi* (Crustacea, Decapoda), from the Lower Pierre Shale, southeastern Montana.—Journal of Paleontology 60:1097–1102.

Eldredge, L. G. 1980. Two species of *Homola* (Dromiacea, Homolidae) from Guam.—Micronesica 16:271–277.

Förster, R., & W. Stinnesbeck. 1987. Zwei neue Krebse, *Callianassa saetosa* n. sp. und *Homolopsis chilensis* n. sp. (Crustacea, Decapoda) aus der Oberkreide Zentral-Chiles.—Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie 27:51–65.

Glaessner, M. F. 1929. Crustacea Decapoda. Fossilium Catalogus. 1. Animalia, Pars 41:1–464, W. Junk, Berlin.

———. 1969. Decapoda. Pp. R399–R533, R626–R628 *in* R. C. Moore, ed., Treatise on invertebrate paleontology, Pt. R, Arthropoda 4, Vol. 2. The Geological Society of America, Inc., and The University of Kansas.

Gordon, I. 1950. Crustacea Dromiacea. Part I. Systematic account of the Dromiacea collected by the "John Murray" Expedition. Part II. The morphology of the spermatheca in certain Dromiacea.—The John Murray Expedition, 1933–34, Scientific Reports, Vol. 9, Zoology and Botany:201–253, 1 plate.

Griffin, D. J. G. 1965. A new species of *Paromola* (Crustacea, Decapoda, Thelxiopidae) from New Zealand.—Transactions of the Royal Society of New Zealand 7(4):85–91, 2 plates.

———, & H. A. Tranter. 1986. The Decapoda Brachyura of the Siboga Expedition, Part VIII, Majidae.—Siboga-Expeditie Monographie 39, C4:1–335, 22 plates.

Guinot, D. 1979. Morphologie et phylogenèse des brachyoures.—Mémoires du Muséum National d'Histoire Naturelle, New Series, Series A, Zoologie 112:1–354, 27 plates.

———. 1985. Crabes bathyaux de l'Île de la Réunion; description de *Cyrtomaia guillei* sp., nov., de *Platypilumnus inermis* sp. nov. et de *Psopheti-*

cus vocans sp. nov. (Crustacea Decapoda Brachyura). Résultats de Campagnes Océanographiques du M.S. "Marion-Dufresne" et de Prospections Littorales de la Vedette "Japonaise."—Comité National Française de Recherches Antarctiques, No. 55 (for 1984):7–31, plates 1–4.

———. 1991. Établissement de la famille des Poupiniidae pour *Poupinia hirsuta* gen. nov., sp. nov. de Polynésie (Crustacea Decapoda Brachyura Homoloidea).—Bulletin du Muséum National d'Histoire Naturelle, Paris, Sér. 4, 12A(3-4, for 1990):577–605.

———, & B. Richer de Forges. 1981. Homolidae, rares ou nouveaux, de l'Indo-Pacifique (Crustacea, Decapoda, Brachyura).—Bulletin du Muséum National d'Histoire Naturelle, Paris, Sér. 4, 3A(2):523–581.

———, & ———. 1982a. Nouvelles récoltes des genres *Cyrtomaia* Miers et *Pleistacantha* Miers (Crustacea, Decapoda, Brachyura).—Bulletin du Muséum National d'Histoire Naturelle, Paris, Sér. 4, 3A(4, for 1981):1087–1125.

———, & ———, 1982b. Révision du genre Indo-Pacifique *Cyrtomaia* Miers, 1886: Campagnes océanographiques du *Challenger*, de l'*Albatross*, du *Siboga* et du *Vauban* (Crustacea Decapoda Brachyura).—Annales de l'Institut Océanographique, N. S. 58, Fasc. 1:5–88.

———, & ———. 1985. Crustacés, Décapodes: Majidae (genres *Platymaia, Cyrtomaia, Pleistacantha, Sphenocarcinus* et *Naxioides*). Résultats des Campagnes Musorstom I et II, Philippines (1976, 1980), Vol. 2.—Mémoires du Muséum National d'Histoire Naturelle, Paris, Sér. A, 133, Zoologie (I & II. Philippines), 4:83–176, 11 plates.

de Haan, W. 1839 Crustacea. *In* P. F. von Siebold, Fauna Japonica sive descriptio animalium, quae in itinere per Japoniam, jussu et auspiciis superiorium, qui summum in India Batavia imperium tenent, suscepto, annis 1832–1830 collegit, notis observationibus et adumbrationibus illustravit, fasc. 4:73–108, plates 25–32, G, H.

Henderson, J. R. 1888. Report on the Anomura collected by H.M.S. Challenger during the years 1873–76.—Report on the Scientific Results of the Voyage of H.M.S. Challenger during the years 1873–76 . . . etc., Zoology 27(69):i–xi, 1–221, 21 plates.

Ihle, J. E. W. 1913. Die Decapoda Brachyura der Siboga-Expedition. I, Dromiacea.—Siboga-Expeditie, Monographie 39*b*:1–96, 4 plates.

International Commission on Zoological Nomenclature. 1987. Official lists and works in zoology. R. V. Melville & J. D. D. Smith (eds.). The International Trust for Zoological Nomenclature, c/o British Museum (Natural History), London, 366 pp.

Jenkins, R. J. F. 1977. A new fossil homolid crab (Decapoda, Brachyura), Middle Tertiary, southeastern Australia.—Transactions of the Royal Society of South Australia 101:1–10.

MacLeay, W. S. 1838. On the brachyurous decapod Crustacea brought from the Cape by Dr. Smith. Pp. 53–71, plates 2, 3 *in* Illustrations of the Annulosa of South Africa . . . etc.; fitted out by The Cape of Good Hope Association for Exploring Central Africa, London.

Manning, R. B., & L. B. Holthuis. 1981. West African brachyuran crabs (Crustacea: Decapoda).—Smithsonian Contributions to Zoology 306:i–xii, 1–379.

Melo, G. A. S. de. 1990. Descrição de *Latreillia williamsi*, sp. n. (Crustacea, Brachyura, Homoloidea), e a occorrēcia da familia Latreilliidae no litoral Brasileiro.—Atlántica, Rio Grande:12(2): 27–34.

Miers, E. J. 1879. On a collection of Crustacea made by Capt. H. C. St. John, R.N., in the Corean and Japanese seas. Part I. Podophthalmia. With an appendix by Capt. H. C. St. John.—Proceedings of the Zoological Society of London, pp. 18–61, 3 plates.

———. 1886. Report on the Brachyura collected by H.M.S. Challenger during the years 1873–76.—Report on the Scientific Results of the Voyage of H.M.S. Challenger during the years 1873–76 . . . etc., Zoology 17(49):i–l, 1–362, 29 plates.

Moffitt, R. B., & J. J. Polovina. 1987. Distribution and yield of the deepwater shrimp *Heterocarpus* resource in the Marianas.—Fishery Bulletin, U.S. 85(2):339–349.

Monod, T. 1956. Hippidea et Brachyura ouest-africains.—Mémoires de l'Institut Français d'Afrique Noire 45:1–674.

Polovina, J. J., R. B. Moffitt, S. Ralston, P. M. Shiota, & H. A. Williams. 1985. Fisheries resource assessment of the Mariana Archipelago, 1982–85.—Marine Fisheries Review 47(4):19–25.

Rathbun, M. J. 1937. The oxystomatous and allied crabs of America.—United States National Museum Bulletin, 166:i–vi, 1–278, 86 plates.

Richer de Forges, B., & D. Guinot. 1988. Description de trois espéces de *Cyrtomaia* Miers, 1886, de Nouvelle-Calédonie et des Iles Chesterfield (Crustacea Decapoda Brachyura).—Bulletin du Muséum National d'Histoire Naturelle, Paris, Sér. 4, 10A(1):39–55.

Sakai, T. 1965. The crabs of Sagami Bay. East-West Center Press, Honolulu, Hawaii, xvi + 200 pp. (English text), 100 plates, 92 pp. (Japanese text), 32 pp. (Bibliography and Indexes).

———. 1976. Crabs of Japan and the adjacent seas. Kodansha Ltd., Tokyo, 773 pp. (English text), 251 plates, 461 pp. (Japanese text).

Samouelle, G. 1819. The entomologist's useful compendium, or an introduction to the knowledge of British insects . . . etc. Printed for Thomas Boys, London, 496 pp.

Serène, R., & P. Lohavanijaya. 1973. The Brachyura (Crustacea: Decapoda) collected by the Naga Expedition, including a review of the Homolidae.—Naga Report 4(4):1–187, 21 plates.

Stimpson, W. 1858. Prodromus descriptionis animalium evertebratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem, a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit. Crustacea Anomoura.—Proceedings of the Academy of Natural Sciences of Philadelphia 10(7):225–252.

Takeda, M., & I. Fujiyama. 1983. Three decapod crustaceans from the Lower Cretaceous Miyako Group, northern Japan.—Bulletin of the National Science Museum, Series C (Geology & Paleontology) 9(4):129–136, 2 plates.

Wicksten, M. K. 1985. Carrying behavior in the family Homolidae (Decapoda: Brachyura).—Journal of Crustacean Biology 5(3):476–479.

Williams, A. B. 1982. Revision of the genus *Latreillia* Roux (Brachyura: Homoloidea).—Quaderni del Laboratorio de Tecnologia della Pesca, Ancona, Italy 3(2–5):227–255.

Wright, C. W., & J. S. H. Collins. 1972. British Cretaceous crabs.—Palaeontographical Society Monographs 126(533):1–114, 22 plates.

Zarenkov, N. A., & I. V. Khodkina. 1981. Decapod crustaceans. Pp. 83–93, 154 *in* A. P. Kusnetsov & A. N. Mironov, eds., Benthos of the submarine mountains Marcus-Necker and adjacent Pacific regions. Academy of Sciences of the USSR, P.P. Shirshov Institute of Oceanology, Moscow. [In Russian.]

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Interannual Variation in Growth Rates and Back-Calculated Birthdate Distributions of Pelagic Juvenile Rockfishes (*Sebastes* spp.) off the Central California Coast

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Abstract.– Young-of-the-year pelagic juvenile rockfish (genus *Sebastes*) were collected during annual surveys in the spring and early summer, 1983–88, off the central California coast. Growth rates and back-calculated birthdate distributions of five species (shortbelly rockfish *S. jordani*, bocaccio *S. paucispinis*, chilipepper *S. goodei*, widow rockfish *S. entomelas*, and yellowtail rockfish *S. flavidus*) were estimated from daily otolith increments.

Interspecific variation in growth rates was evident, with bocaccio exhibiting the fastest growth (0.56–0.97 mm/day) and yellowtail rockfish growing slowest (0.19–0.46 mm/day). Growth rates of all species varied among years. Comparisons of annual growth performance, measured by predicting standard length at a selected standard age, revealed strong positive interannual covariation among the five species studied; in general, growth was relatively good in 1987 and was poor in 1985.

Back-calculated birthdate distributions also revealed strong positive interannual covariation among these species; most distributions were unimodal. The years 1985 and 1988 were characterized by distributions that were centered early in the year; whereas in 1986 (and possibly in 1983) these distributions occurred later.

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Understanding recruitment fluctuations and the interplay of factors affecting the establishment of year-class strength is the single most challenging issue in fisheries today (Rothschild 1986). In particular, rockfishes of the genus *Sebastes* are known to exhibit large fluctuations in recruitment (Leaman and Beamish 1984), wherein a single dominant year-class can sustain a fishery for a number of years. Rockfishes are an important component of the west coast groundfish fishery, with combined 1988 landings of 35,000 MT (PFMC 1989). Historically, rockfish stock assessments have relied almost exclusively on catch-at-age data (e.g., Hightower and Lenarz 1989); such analyses do not perform well in the absence of auxiliary information (e.g., an index of pre-recruit abundance). Knowledge of mechanisms affecting first-year survival could improve our ability to predict recruitment, which in turn could have major implications to the management of this group (Deriso et al. 1985, Methot 1989, but see Walters 1989).

In some situations starvation and food limitation have been shown to control larval abundance (Lasker 1981), although predation is believed to be important in others (reviewed in Sissenwine 1984, Bailey and Houde 1989). In either case, if mortality decreases with increasing size (Miller et al. 1988), larval and pelagic juvenile growth rates can have a major impact on survivorship during the first year of life. This is because fast-growing fish are exposed to high mortality rates for shorter periods of time (Houde 1987).

As part of an ongoing study to monitor annual fluctuations in the abundance of young-of-the-year pelagic juvenile rockfishes inhabiting the coastal waters off central California, the growth of five species (shortbelly rockfish *S. jordani*, bocaccio *S. paucispinis*, chilipepper *S. goodei*, widow rockfish *S. entomelas*, and yellowtail rockfish *S. flavidus*) was assessed through the study of otolith daily-increment microstructure formed during the pelagic larval and juvenile life stages (Jones 1986). Intraspecific differences in growth performance over the period 1983–88 were then examined statistically and trends were compared among species.

Birthdate frequency distributions of the fish that survived from birth to the time of sampling were back-calculated from aged subsamples, length measurements, and known dates of capture (Bolz and Lough 1983). These projected distributions were compared intraspecifically among years to evaluate whether the preponderance of juvenile survivors came from larvae that were extruded early or late in the season. Birthdate distributions were also compared among species to reveal the extent of interspecific covariation in annual survivorship.

Methods

Midwater trawl collections

Annual 30-day cruises aboard NOAA's R/V *David Starr Jordan* began in 1983 and were conducted during late spring (May–June), a time when most pelagic-stage juvenile rockfishes are identifiable to species, but prior to their settling to nearshore and benthic habitats. The sampling gear used was a midwater trawl with a 26 m headrope and 169 m^2 net opening, equipped with a 0.945 cm (3/8″) inner liner. A standard haul consisted of a 15-min nighttime tow at a depth of 30 m covering a distance of roughly 1 km. Additional tows were made at other depths (i.e., 10 and 100 m) as time and bottom topography permitted.

From 1983 to 1985, the survey was designed to sample from nearshore waters out to a distance of 55 km (30 nmi) along transects located at 31 km intervals perpendicular to the coast. Sampling began at Pt. Sur (36°18′N) and continued northward until completion of the cruise. In 1986, the sampling design was modified to permit three "sweeps" through a study area bounded by Cypress Pt. (36°35′N) and Pt. Reyes (38°10′N) (Table 1). Four additional cruises were conducted in April of 1985–88. These cruises ranged from 5 to 10 days in length and were limited to the Gulf of the Farallones (1985–86), or covered one complete sweep of the study area (1987–88). Trawls were conducted at 5–7 stations per night along 7 transects during a sweep. Wyllie Echeverria et al. (1990) discuss the survey methodology in greater detail.

As many as 24 species of pelagic-stage juvenile rockfish were collected during a single cruise. All specimens were tentatively identified and frozen at sea. On rare occasions catches were subsampled when they were too large to enumerate. After 1987, length compositions of large trawl catches were based upon expansion from measured subsamples of each species.

Otolith preparation and analysis

In the laboratory, species identifications were confirmed and fish were measured to the nearest 1.0 mm standard length (SL). For this study, the most important species were selected for age determination. A subsample of juveniles, measured to the nearest 0.1 mm, was selected for daily age analysis based on the size range encountered on each cruise. Specimens were selected at 0.5 mm intervals from the smallest to largest. The sagittal otoliths were removed, cleaned, and adhered concave (lateral)-side-down onto glass microslides using clear nail polish. To reveal the inner microstructure, otoliths were ground with wet 300–600 grit sandpaper and etched with HCl (Brothers et al. 1976).

Table 1

Summary of sampling dates for juvenile rockfish cruises. Asterisks indicate trawls limited to Gulf of the Farallones.

Year	Sweep	Dates	Stations
1983	1	8–24 June	18
1984	1	12–27 June	25
1985	1*	10–16 April	18
	2	31 May–30 June	37
1986	1*	13–22 April	30
	2	3–11 June	33
	3	11–18 June	28
	4	20–25 June	28
1987	1	10–20 April	34
	2	23 May–1 June	33
	3	2–12 June	34
	4	12–21 June	33
1988	1	16–22 April	28
	2	22–31 May	33
	3	2–9 June	33
	4	11–18 June	31

A compound microscope with 40 and 100× objectives was used during otolith examination. Immersion oil was applied to the otolith, which was illuminated with polarized light. A closed circuit television camera was mounted on top of the microscope and the image was relayed to a video monitor. A digitizer with a precision of 0.13 μm was interfaced with the monitor and a microcomputer to accurately measure and record daily increments (e.g., McGowan et al. 1987). In combination, the equipment yielded an 800–2000× on-screen magnification range.

A computer program assisted in recording the distance from the nucleus to each increment, measured along the growth axis running from the focus to the postrostral margin. On occasion the periodic bipartite microstructure of daily increments was difficult to resolve within short (~50 μm) segments of the otolith. In these cases their number and width were interpolated by averaging the widths of the rings immediately preceding and following that segment, and dividing the mean into the segment length. Usually such averaging involved only about 10% of the total increments observed. In most cases (~80%), only one otolith was used unless it was damaged or destroyed during preparation. Otoliths were read only once due to the destructive nature of the preparation method.

A photomicrograph of a shortbelly rockfish otolith (Fig. 1) shows increments that we interpreted to be produced daily. A dark ring followed by narrow, closely spaced rings was used as the starting point for enumeration of increments. The time of first increment formation is species-specific. Cases are known where fish larvae form the first increment at hatch, yolksac absorption, first feeding, or at other times (Jones 1986). Penney and Evans (1985), in their study of larval redfish (*Sebastes* spp.) off Newfoundland, noted a "heavy ring composed of a wide, translucent band followed by a prominent, high-contrast dark band" which they used as the first increment for age determination. Since all pre-extrusion larvae lacked the dark band and all planktonic larvae possessed it (some as young as 1 day), they assumed that it formed at the time of extrusion. Structurally, their extrusion check was quite similar to the marks seen in this study (Fig. 1). They, like us, also observed a number of thin, weakly expressed "pre-extrusion rings" laid down prior to the first increment (see also Campana et al. 1987). There are instances in which small (~4.8–5.0 mm) field-caught planktonic larvae of shortbelly rockfish lack the conspicuous first increment (T. Laidig, SWFC Tiburon Lab., pers. commun.). Faced with this uncertainty, we conclude that the first increment used in our counts forms some time between extrusion and first feeding. The distance of this first ring from the center of the focus varied among species (i.e., 12–17 μm), but was consistent within a species. The first few increments laid down after this early check ring typically were about 0.5 μm in width and they increased in size thereafter.

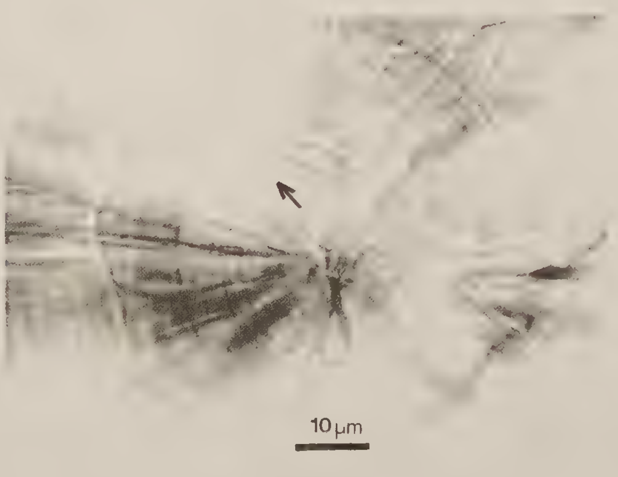

Figure 1
Photomicrograph of a shortbelly rockfish otolith showing the first increment (arrow) and subsequent development of increment microstructure.

Several lines of evidence indicate that the periodicity of otolith increments we counted was daily. For one, all back-calculated birthdate distributions fell within known annual parturition (spawning) seasons (Wyllie Echeverria 1987, MacGregor 1986). In addition, results from a separate study that sequentially sampled larval and juvenile shortbelly rockfish in 1989 showed that one increment was deposited each day from May to June (Laidig et al. In press). Lastly, Yoklavich and Boehlert (1987) validated the existence of daily growth increments in juvenile *S. melanops* using autoradiography to detect injected ^{45}Ca, as well as by tetracycline injection.

Under the assumption that one increment was produced each day, growth rate was measured by regressing SL (mm) against estimated age (days). Analysis of covariance was used to test for differences in the relationship of SL and age within and among years. When differences were found, pairwise comparisons of class means were made using the least significant difference (LSD) test (Snedecor and Cochran 1967). This test maintains the comparisonwise error rate at $\alpha = 0.05$, but, depending on the number of means compared, increases the experimentwise probability of committing a Type I error. In addition, indices of annual growth performance were obtained by predicting standard length at a selected standard age using regression statistics from each individual year. These were evaluated using principal component analysis (Green 1978) to reveal interdependency among the data. In this analysis, species were treated as variables, years comprised cases, and components were computed from the correlation matrix.

Back-calculated birthdate distributions of the fish that survived until the time of sampling were obtained by: (1) linearly regressing age on SL using the subsample of aged fish, (2) using the regression equation obtained to estimate the age of fish sampled during May–June cruises only, (3) back-calculating to the calendar date of first increment formation by difference (calendar date of capture minus age in days), and (4) aggregating the data into frequency distributions. Although with this approach some lengths were excluded, data from April cruises were not used due to the sporadic sampling (temporally and spatially) that occurred. Back-calculated birthdate distributions were compared within and among years, as well as among species.

Results

In some cases, analysis of covariance (ANCOVA) revealed statistically significant differences in the relationship of standard length and age among the various sweeps conducted within a year (i.e., bocaccio in 1987, chilipepper in 1988, widow rockfish in 1987, and yellowtail rockfish in 1986). It is notable, however, that these cases represented only 4 of the 15 species-year combinations for which data were available. Further examination of the data revealed that in one of these cases significance was due to a very small sample obtained during one sweep. Moreover, in the other three instances there was no regular pattern of either increasing or decreasing growth rate as the season progressed and the magnitude of differences was small. For these reasons a single regression equation describing the annual growth of each species was generated by pooling the age data obtained in a year, ignoring the sweep of origin.

Growth

Shortbelly rockfish There was a linear relationship between standard length (mm) and age (days) for shortbelly rockfish over the size range collected in each year during 1983–88 (Fig. 2). A simple linear growth model was fit to each year individually (Table 2). Annual estimates of pelagic juvenile shortbelly rockfish growth rate ranged from 0.524 mm/day in 1985 to 0.638 mm/day in 1983. Results from ANCOVA (Table 3) showed that significant differences (P 0.019) occurred in annual growth rates (i.e., slopes) among the six years sampled. Growth rates were relatively low in 1985 and 1986, were medium in 1984 and 1988, and were high in 1983 and 1987. To test for differences in estimates of annual growth rate, pairwise comparisons were made using LSD tests (Fig. 3).

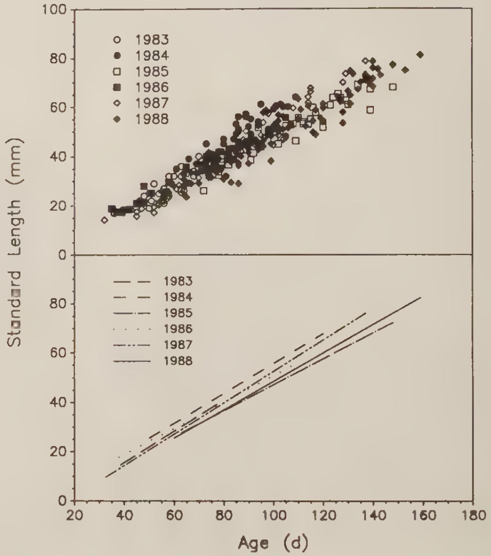

Figure 2

Scattergrams of shortbelly rockfish *Sebastes jordani* standard length on age for each year, 1983–88 (upper), with fitted linear regressions to each year of data (lower).

Table 2

Annual regression statistics for the linear growth model.

Rockfish species	Year	N	Slope (mm/d)	Slope (SE)	Intercept (mm)	Intercept (SE)	r^2
Shortbelly	1983	32	0.6377	(0.0650)	−9.7612	(3.9387)	0.763
	1984	52	0.6025	(0.0487)	−4.4985	(4.1709)	0.754
	1985	40	0.5239	(0.0258)	−5.3236	(2.7594)	0.915
	1986	34	0.5316	(0.0199)	−2.4195	(1.4332)	0.957
	1987	53	0.6349	(0.0183)	−10.9365	(1.6089)	0.959
	1988	91	0.5735	(0.0197)	−8.7806	(2.0927)	0.905
Bocaccio	1984	50	0.6774	(0.0382)	−16.8644	(3.9810)	0.868
	1985	19	0.9737	(0.1076)	−56.4082	(12.0249)	0.828
	1986	48	0.5627	(0.0226)	−11.2418	(1.7521)	0.931
	1987	90	0.7346	(0.0209)	−24.6335	(1.9917)	0.934
	1988	53	0.7339	(0.0449)	−30.7046	(5.5366)	0.840
Chilipepper	1985	36	0.4028	(0.0336)	−2.5392	(3.3381)	0.808
	1986	27	0.3990	(0.0365)	0.3622	(2.8803)	0.827
	1987	74	0.5553	(0.0190)	−9.9867	(2.0029)	0.922
	1988	74	0.5500	(0.0239)	−16.8179	(2.7082)	0.881
Widow	1985	25	0.5647	(0.0762)	−13.9356	(8.8497)	0.705
	1986	9	0.2986	(0.0978)	13.2109	(9.5706)	0.571
	1987	45	0.6070	(0.0316)	−13.4434	(3.0735)	0.896
	1988	49	0.5696	(0.0231)	−13.2175	(2.7276)	0.928
Yellowtail	1985	18	0.1944	(0.0830)	20.4415	(9.6333)	0.255
	1986	9	0.4634	(0.0263)	−6.3261	(2.2973)	0.978
	1987	23	0.4620	(0.0655)	−1.7767	(6.9320)	0.703
	1988	24	0.4016	(0.0353)	−1.9092	(3.7319)	0.855

Table 3

Analyses of covariance testing for differences in slopes and adjusted means (i.e., elevation) of annual (1983–88) linear growth curves for each of five species of pelagic juvenile rockfish. Tests for adjusted means were done only when the test of equality of slope was not significant. Dependent variable = SL, covariate = age, treatment variable = year.

Rockfish species Source	df	Sum of squares	Mean square	F	*P*
Shortbelly					
Equality of slopes	5	219.30	43.86	2.74	0.019
Error	290	4,637.14	15.99		
Bocaccio					
Equality of slopes	4	705.01	176.25	6.16	0.001
Error	250	7,157.92	28.63		
Chilipepper					
Equality of slopes	3	262.68	87.56	5.00	0.002
Error	203	3,557.01	17.52		
Widow					
Equality of slopes	3	75.63	25.21	1.64	0.184
Error	120	1,845.44	15.38		
Equality of adjusted means	3	392.41	130.80	8.38	0.001
Error	123	1,921.07	15.62		
Yellowtail					
Equality of slopes	3	57.41	19.14	2.13	0.104
Error	66	591.95	8.97		
Equality of adjusted means	3	798.09	266.03	28.27	0.001
Error	69	649.36	9.41		

Bocaccio The data presented in Figure 4 show the relationship between standard length and age for the aged subsamples of pelagic juvenile bocaccio in each year during 1984–88. No data were available for 1983. There is some suggestion of curvilinearity in the data, especially in the youngest stages of growth, but this cannot be confirmed due to annual differences in the age domain sampled. For example, specimens ranged in age from 35 to 113 days during 1986, whereas in 1985 they ranged from 84 to 131 days. Thus, differences in slope between these years may be due to a year effect in the linear model, or to violation of the linearity assumption. In spite of the suggestion of nonlinearity in the data when pooled over years, the linear model was used to conform with the analyses performed on the other four species studied and because it fits well on a year-by-year basis.

A simple linear growth model was fit to individual years (Table 2). During the period studied, the highest growth rate

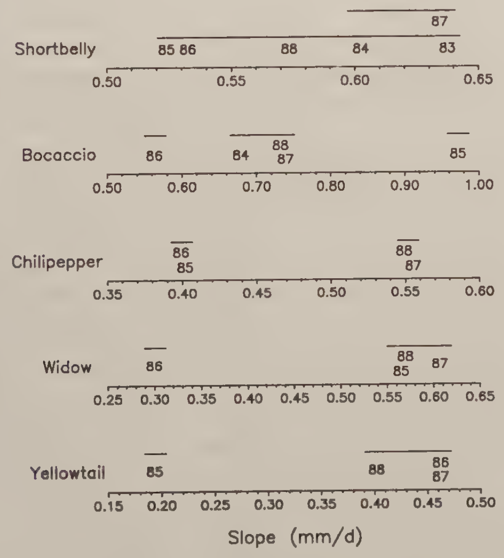

Figure 3

Results of all possible pairwise least-significant-difference tests of annual differences in growth rate (slope) for each species studied. A bar over and connecting different years (1983–88) indicates lack of significance. No adjustments were made to control the experiment-wide probability of Type I error.

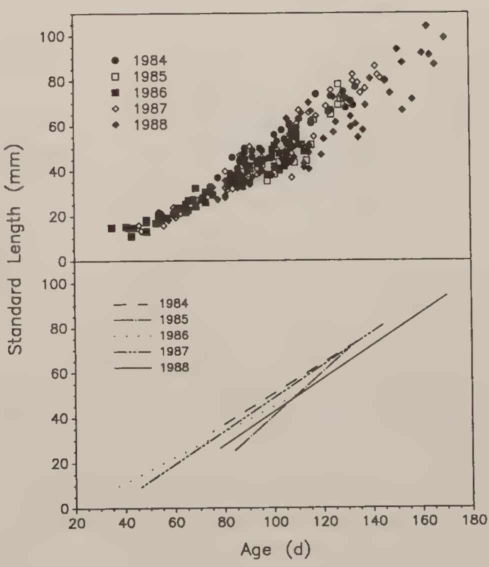

Figure 4

Scattergrams of bocaccio *Sebastes paucispinis* standard length on age for each year, 1984–88 (upper), with fitted linear regressions to each year of data (lower).

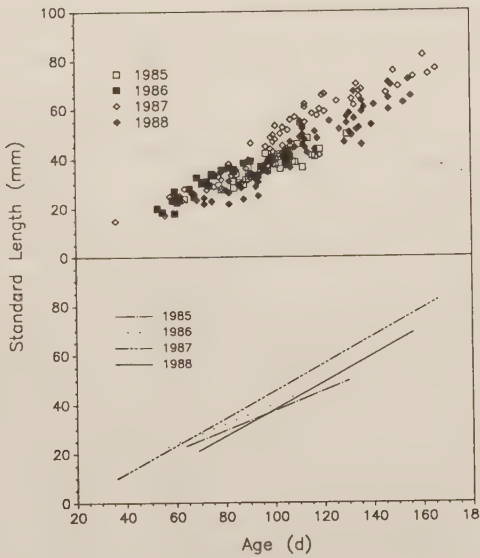

Figure 5

Scattergrams of chilipepper *Sebastes goodei* standard length on age for each year, 1985–88 (upper), with fitted linear regressions to each year of data (lower).

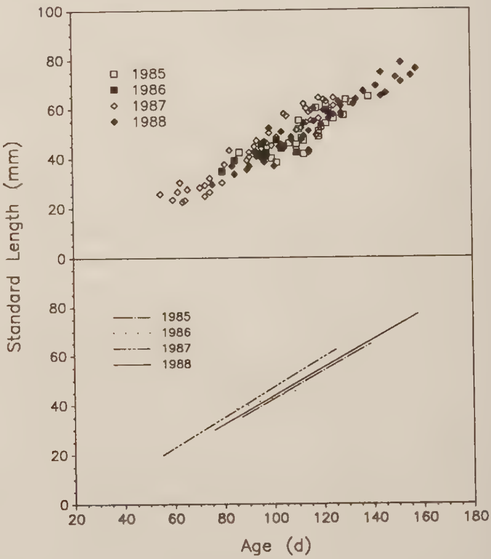

Figure 6

Scattergrams of widow rockfish *Sebastes entomelas* standard length on age for each year, 1985–88 (upper), with fitted linear regressions to each year of data (lower).

occurred in 1985 (0.974 mm/day), whereas the lowest growth rate (0.563 mm/day) was seen in 1986. Results of ANCOVA (Table 3) show that significant differences (*P* 0.001) in growth rate occurred among years. Results of all possible pairwise LSD tests comparing annual slope estimates (Fig. 3) show that growth in 1985 was distinctly fast. Growth rates were relatively low in 1986 and were moderate and similar in 1984, 1987, and 1988.

Chilipepper Sufficient numbers of fish were collected during 1985–88. Standard length and age data from these years (Fig. 5) indicate an apparent linear relationship. Regression statistics resulting from fitting each year's data to the linear growth model are provided in Table 2. Annual growth rates ranged from a low of 0.399 mm/day in 1986 to a high of 0.555 mm/day in 1987. Results from ANCOVA (Table 3) show that annual differences exist in growth rate (*P* 0.002); pairwise LSD comparisons of slopes (Fig. 3) indicate a very clear separation between the slow growth that occurred in 1985–86 and the relatively fast growth in 1987–88.

Widow rockfish Like chilipepper, widow rockfish were collected in sufficient numbers only in the years 1985–88. The scatter of data (Fig. 6) shows an apparently linear increase in standard length, at least over the range of ages sampled. A problem with the data is that in 1986 only 9 fish were collected, with ages ranging 80–110 days. This resulted in a marked reduction in age contrast (30 days).

The data from each year were fitted separately with linear regression (Table 2), with estimates of growth rate ranging from 0.299 mm/day in 1986 (*N* 9) to 0.607 mm/day in 1987. When ranked, the descending sequence of estimated annual growth rates (i.e., slopes) was: 1987>1988>1985>1986. Results of ANCOVA (Table 3), however, indicated that slopes did not vary significantly among years (*P* 0.184), although all possible pairwise LSD comparisons (Fig. 3) showed that growth rate in 1986 was slower than in other years. The reason the ANCOVA failed to reveal differences in slope among years was likely due to a small sample size and low age contrast in 1986. An F-test for annual differences in adjusted means (i.e., elevation) did reveal significant differences (Table 3, *P* 0.001). Pairwise LSD comparisons of annual adjusted means indicated that pelagic juveniles were larger in 1987 than in other years. When ranked, the descending sequence of annual adjusted means was: 1987>1986>1988 >1985.

Yellowtail rockfish Juvenile yellowtail rockfish comprised the fewest specimens collected of the five species studied. Sufficient specimens for growth analysis were collected only in the years 1985–88. The scattergram (Fig. 7) shows the smallest range in standard length and age observed. This problem is exemplified in 1985 when the ages ranged only 107–133 days.

The data were fitted by linear regression for each year (Table 2) resulting in estimates of growth rate that ranged from 0.194 mm/day in 1985 to 0.463 mm/day in 1986. The descending sequence of estimated annual growth rates of yellowtail rockfish was: 1986>1987>1988>1985. Results of ANCOVA (Table 3) testing for annual differences in slope were borderline (*P* 0.104); all possible pairwise LSD comparisons (Fig. 3) showed that growth rate in 1985 was slower than in other years. An F-test of annual differences in adjusted means was significant (Table 3, *P* 0.001). Like widow rockfish, results from all possible pairwise comparisons of yearly adjusted mean standard length indicated that yellowtail rockfish juveniles were larger in 1987 than in other years, with fish sampled in 1986 and 1988 somewhat larger (*P* 0.05–0.10) than those taken in 1985. The rank order of adjusted mean standard length was identical to that observed in widow rockfish (i.e., 1987>1986>1988>1985).

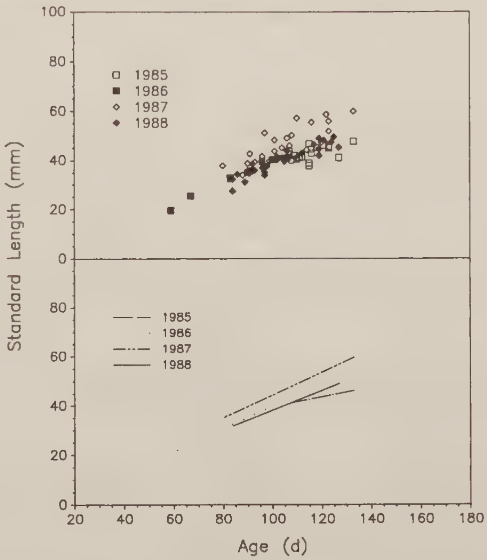

Figure 7
Scattergrams of yellowtail rockfish *Sebastes flavidus* standard length on age for each year, 1985–88 (upper), with fitted linear regressions to each year of data (lower).

Annual growth performance

The data presented thus far make it difficult to compare and contrast the growth of the five species on an annual basis. For example, results from bocaccio (lower panel in Figure 4) show that 1985 was characterized by the highest growth rate (0.974 mm/day). Even so, 90-day-old fish in 1985 were estimated to be smaller than in any other year. In this situation it is possible that poor growth performance during early-life-history stages, prior to those sampled, had no lasting effect on growth at the time of sampling. There may even have been some form of compensatory growth response.

To overcome this problem we compared annual growth performance within and among species by estimating length at a selected standard age with the regression statistics presented in Table 2. This is functionally equivalent to integrating annual growth rates up to the selected standard age, providing a common basis for comparison among years. The standard age for each species was determined from the range of ages sampled in the various years. Standard ages were selected to prevent extrapolation of the regressions. Specific ages selected were: shortbelly rockfish 70 days, bocaccio 100 days, chilipepper 90 days, widow rockfish 100 days, and yellowtail rockfish 107 days.

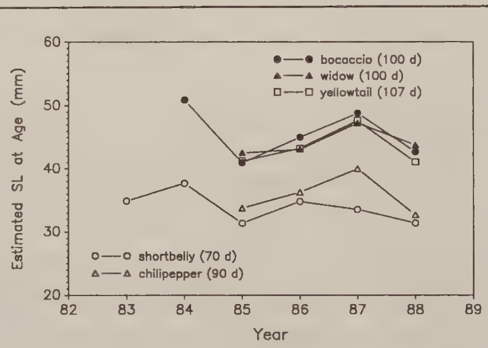

Figure 8
Annual estimates (1983–88) of standard length at standardized ages of shortbelly, bocaccio, chilipepper, widow, and yellowtail rockfishes.

Results show coherent differences in growth performance from year to year (Fig. 8). Among the five species over the last four years of the study, 1985 consistently produced the smallest fish and, with the exception of shortbelly rockfish, 1987 yielded the largest fish observed. Although only represented by two

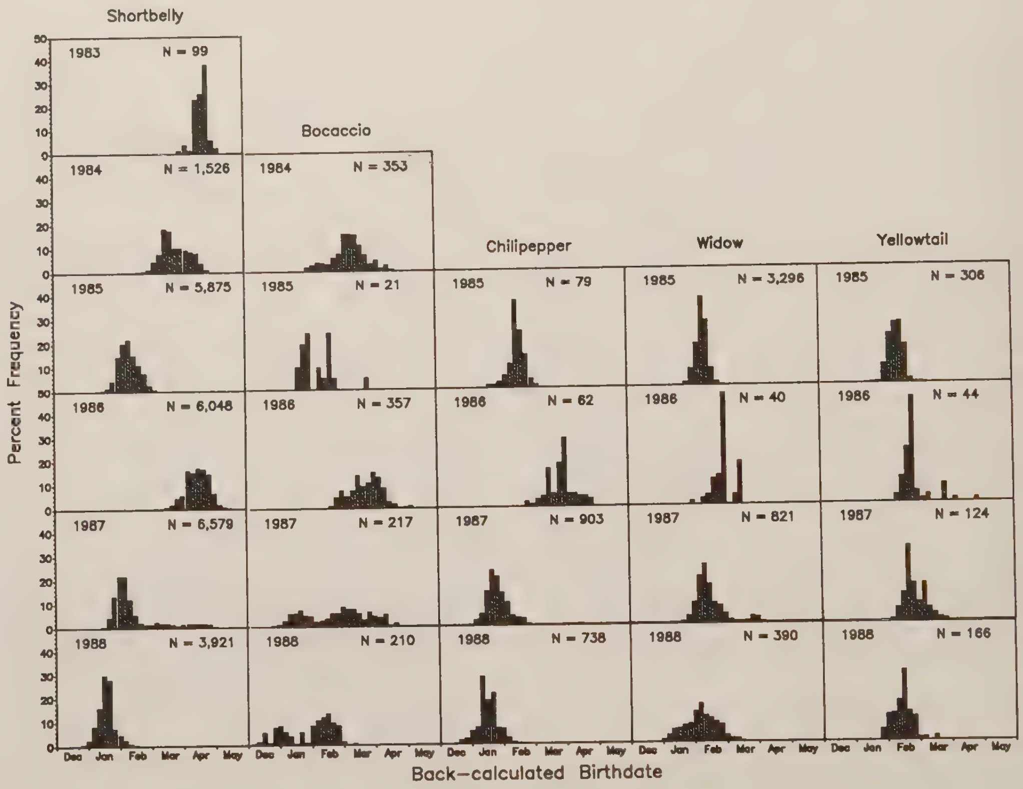

Figure 9

Composite annual back-calculated birthdate distributions of shortbelly, bocaccio, chilipepper, widow, and yellowtail rockfishes (1983–88).

species (bocaccio and shortbelly rockfish), 1984 produced faster growth than in any other year.

Overall, growth performance shows remarkable coherency in this time series. This conclusion is further reinforced with results from principal component analysis. Following ordination, 83.3% of the variation in growth-performance standard scores was accounted for by the first principal component (λ_1 4.16). First component scores (ξ_1) for each year were ranked in descending order as follows: 1987 (ξ_1 2.74)>1986 (ξ_1 0.36)>1988 (ξ_1 −1.40)>1985 (ξ_1 −1.71). These values follow the general pattern evident in Figure 8.

Back-calculated birthdate distributions

As with the aged subsample data, the birthdate frequency distributions that were generated from length-frequency data were pooled across sweeps within each year, even though in some cases significant differences occurred. Although sweep-to-sweep differences would be useful in elucidating within-season patterns of mortality, movement, and growth, we ignored them because an analysis of the components of variance showed that, with the exception of yellowtail rockfish, variation of this kind was quite minor in comparison to yearly fluctuations in birthdate distributions.

Results of back-calculating time of birth (Fig. 9) show that, typically, surviving juveniles were born during a two-month period. For most species-year combinations, a unimodal distribution is evident. Bocaccio display somewhat broader birthdate distributions than the other species, perhaps reflecting their multiple spawning capability in southern California waters (MacGregor 1970). Positive skewness in the birthdate distributions of all five species was evident in 1987, being particularly marked in shortbelly, chilipepper, and widow rockfish. What is most striking in these data, however, is the broad coherence among the species in the yearly shifts that occurred in the distributions (Fig. 10). For example, 1986 was a year in which successful parturition occurred late in the season for all species examined. Conversely, 1985 and 1988 were years marked by earlier birthdate distributions.

Principal component analysis demonstrates the great degree to which these data are coherent in time (1985–88). Results show that 92.9% of the variation in mean back-calculated calendar birthdate standard scores was accounted for by the first principal component (λ_1 4.64). Given the tight coupling that occurred between bocaccio and shortbelly rockfish in 1984–85, these values may well have been higher if data had been available for all species in all years (1983–88). First component scores for each year were ranked in descending order as follows: 1986 (ζ_1 2.93)>1987 (ζ_1 0.13)>1985 (ζ_1 −1.16)>1988 (ζ_1 −1.89). This sequence mirrors the interannual shifting of distributions evident in Figures 9 and 10.

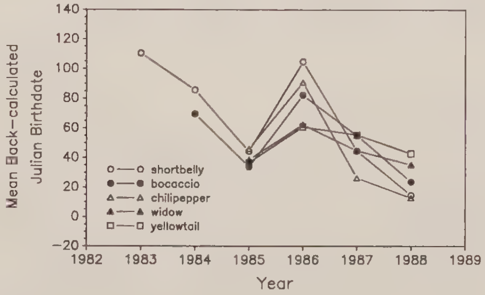

Figure 10

Annual trends (1983–88) in the means of back-calculated birthdate distributions for shortbelly, bocaccio, chilipepper, widow, and yellowtail rockfishes.

Discussion

Growth

Growth rates of field-collected larval and pelagic juvenile *Sebastes* spp. have been determined by others using otolith microstructure (reviewed in Kendall and Lenarz 1987, Moser and Boehlert 1991). It is noteworthy that in all cases a linear growth model fitted the data best, similar to results reported here (Figs. 2, 4–7). Data for *S. melanostomus* (*N* 4) indicated that at 15–30 mm SL the growth rate was 0.24 mm/day (Moser and Ahlstrom 1978). Research on *S. diploproa* (Boehlert 1981) showed a growth rate of 0.19 mm/day for fish 10–40 mm SL. Both studies were conducted off southern California. Penney and Evans (1985) estimated that redfish (composite of *S. marinus*, *S. mentella*, and *S. fasciatus*) from the northwest Atlantic grew at the rate of 0.11–0.16 mm/day when in the range 8–25 mm TL.

These growth rates are somewhat lower than those presented in Table 2. Our data show growth rates ranging 0.52–0.64 mm/day for shortbelly rockfish, 0.56–0.97 mm/day for bocaccio, 0.40–0.56 for chilipepper, and 0.30–0.61 mm/day and 0.19-0.46 mm/day for widow and yellowtail rockfishes, respectively. This is likely due to the span of ages and/or sizes caught, since our fish were larger and older than in these other studies. It is conceivable, however, that the growth rates of pelagic juvenile *Sebastes* spp. along the central California coast are enhanced in response to superior feeding conditions and increased ration (Brett 1979), a consequence of elevated production associated with coastal upwelling (Smith 1968). Dietary studies of these fishes show that they feed primarily on various life stages of euphausiids and calanoid copepods (Reilly et al. In prep.).

Interannual variation in growth performance has been implicated as a major factor affecting year-class strength (Miller et al. 1988). Houde (1987) showed with simple calculations that, in some situations, a doubling of the instantaneous growth rate during the early life history can increase the number of recruits by nearly 100-fold. Moderate and significant interannual variations in growth rates/performance were evident for the species in this study. Likewise, widow rockfish year-class strength has varied 10-fold during the 1974–89 period (Hightower and Lenarz 1989). These results are, therefore, consistent with the hypothesis that fluctuations in rockfish recruitment are due, at least in part, to interannual variation in growth rate.

Birthdate distributions

Back-calculation of birthdate distributions using daily increment data has been reported before (e.g., Bolz and Lough 1983, Brothers et al. 1983, Methot 1983, Jones 1985, Penney and Evans 1985, Thorrold 1989). One difficulty with this approach is that estimates of the numbers born by date should be adjusted for differences in mortality (Penney and Evans 1985), i.e., to have appeared in our samples, older juveniles must have survived for a longer period of time than younger ones. However, without an estimate of early larval and juvenile mortality rates we were unable to adjust for this effect. In this sense, the histograms presented in Figure 9 represent the birthdate distributions of the fish that survived to the time of sampling.

The distributions are also influenced by other factors. For example, there are differences among the species in duration of the pelagic phase. This is especially true for widow and yellowtail rockfish, which tend to settle at a relatively young age. Results may also be biased if parturition occurs unusually late in the year. In this case the larvae/juveniles might not be large enough to be captured by the gear we used. However, our sampling occurred annually at similar times, and marked differences in the distributions were still noted. The early birthdate distributions characterizing bocaccio, chilipepper, and shortbelly rockfish in 1988 were due to the prevalence of relatively old fish, whereas fish sampled in 1986 were relatively young. Although these shifts may be influenced by settlement and gear selectivity, they nonetheless provide a conservative representation of interannual differences.

Two possible hypotheses accounting for interannual variation in the means of back-calculated birthdate distributions are (1) annual variation in the seasonal timing of parturition, and (2) year-specific seasonal variation in the expression of mortality rates within fixed parturition seasons. Although at present we have no basis to distinguish between these two alternatives, this topic is currently under detailed investigation.

Oceanographic conditions

It is well known that temperature has a major influence on larval growth at sea. There is evidence that sea-surface temperature (SST) affects the growth performance of pelagic juvenile rockfish off central California (lat. 36–39°). In this area mean January SST from 1983–87 (Cole and McLain 1989) was positively associated with growth performance. For example, in 1984 shortbelly rockfish were estimated to be 37.7 mm SL at a standard age of 70 days. This represented this species' best growth during the 1983–88 period, and in this year mean January SST was a very warm 13.12°C. In contrast, in 1985, when mean January SST was at its lowest value in the time series (12.05°C), estimated length at age was lowest also (31.3 mm SL).

Similar to growth, there is evidence that sea-surface temperature has a strong influence on interannual shifting of back-calculated birthdate distributions. Cold years were associated with early successful parturition. Our results show that for shortbelly rockfish the annual mean of the birthdate distribution was at its minimum in 1985 (8 February) when mean January SST was only 12.05°C. By comparison, in 1983 (an El Niño year) the birthdate mean was at its maximum value (21 April) in association with warm January SST (13.16°C). These findings are intriguing and form the basis of ongoing investigations into the establishment of year-class strength in *Sebastes* spp.

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Citations

Bailey, K.M., and E.D. Houde
1989 Predation on eggs and larvae of marine fishes and the recruitment problem. Adv. Mar. Biol. 25:1–82.

Boehlert, G.W.
1981 The effects of photoperiod and temperature on laboratory growth of juvenile *Sebastes diploproa* and a comparison with growth in the field. Fish. Bull., U.S. 79:789–794.

Bolz, G.R., and R.G. Lough
1983 Growth of larval Atlantic cod, *Gadus morhua*, and haddock, *Melanogrammus aeglefinus*, on Georges Bank, spring 1981. Fish. Bull., U.S. 81:827–836.

Brett, J.R.
1979 Environmental factors and growth. *In* Hoar, W.S., D.J. Randall, and J.R. Brett (eds.), Fish physiology, Vol. VIII: Bioenergetics and growth, p. 599–675. Academic Press, NY.

Brothers, E.B., C.P. Mathews, and R. Lasker
1976 Daily growth increments in otoliths from larval and adult fishes. Fish. Bull., U.S. 74:1–8.

Brothers, E.B., E.D. Prince, and D.W. Lee
1983 Age and growth of young-of-the-year bluefin tuna, *Thunnus thynnus*, from otolith microstructure. *In* Prince, E.D., and L.M. Pulos (eds.), Proceedings, International workshop on age determination of oceanic pelagic fishes: Tunas, billfishes, and sharks, p. 49–59. NOAA Tech. Rep. NMFS 8.

Campana, S.E., J.A. Gagné, and J. Munro
1987 Otolith microstructure of larval herring (*Clupea harengus*): Image or reality. Can. J. Fish. Aquat. Sci. 44: 1922–1929.

Cole, D.A., and D.R. McLain
1989 Interannual variability of temperature in the upper layer of the North Pacific eastern boundary region, 1971–1987. Tech. Memo. NOAA-TM-NMFS-SWFC-125, Southwest Fish. Sci. Cent., La Jolla, 10 p.

Deriso, R.B., T.J. Quinn II, and P.R. Neal
1985 Catch-age analysis with auxiliary information. Can. J. Fish. Aquat. Sci. 42:815–824.

Green, P.E.
1978 Analyzing multivariate data. Dryden Press, Hinsdale, IL, 519 p.

Hightower, J.E., and W.H. Lenarz
1989 Status of the widow rockfish fishery. Appendix C *In* Status of the Pacific coast groundfish fishery through 1989 and recommended acceptable biological catches for 1990. Pac. Fish. Manage. Counc., Portland, 50 p.

Houde, E.D.
1987 Fish early life dynamics and recruitment variability. *In* Hoyt, R.D. (ed.), Proc., 10th annual larval fish conference, p. 17–29. Am. Fish. Soc. Symp. 2, Bethesda.

Jones, C.
1985 Within-season differences in growth of larval Atlantic herring, *Clupea harengus*. Fish. Bull., U.S. 83:289–298.
1986 Determining age of larval fish with the otolith increment technique. Fish. Bull., U.S. 84:91–103.

Kendall, A.W. Jr., and W.H. Lenarz
1987 Status of early life history studies of northeast Pacific rockfishes. *In* Proceedings, International rockfish symposium, October 1986, Anchorage, Alaska, p. 99–128. Alaska Sea Grant Rep. 87-2, Univ. Alaska, Fairbanks.

Laidig, T.E., S. Ralston, and J.R. Bence
In press Dynamics of growth in the early life history of shortbelly rockfish, *Sebastes jordani*. Fish. Bull., U.S. 89(4).

Lasker, R.
1981 Factors contributing to variable recruitment of the northern anchovy (*Engraulis mordax*) in the California current: Contrasting years, 1975 through 1978. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 178:375–388.

Leaman, B.M., and R.J. Beamish
1984 Ecological and management implications of longevity in some northeast Pacific groundfishes. Int. North Pac. Fish. Comm., Bull. 42:85–97.

MacGregor, J.S.
1970 Fecundity, multiple spawning, and description of the gonads in *Sebastodes*. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 596, 12 p.
1986 Relative abundance of four species of *Sebastes* off California and Baja California. Calif. Coop. Oceanic Fish Invest. Rep. 27:121–135.

McGowan, M.F., E.D. Prince, and D.W. Lee
1987 An inexpensive microcomputer-based system for making rapid and precise counts and measurements of zonations in video displayed skeletal structures of fish. *In* Summerfelt, R.C., and G.E. Hall (eds.), The age and growth of fish, p. 385–395. Iowa State Univ. Press, Ames.

Methot, R.D. Jr.
1983 Seasonal variation in survival of larval northern anchovy, *Engraulis mordax*, estimated from the age distribution of juveniles. Fish. Bull., U.S. 81:741–750.
1989 Synthetic estimates of historical abundance and mortality of northern anchovy. *In* Vetter, E., and B. Megrey (eds.), Mathematical analysis of fish stock dynamics: Reviews and current applications, p. 66–82. Am. Fish. Soc. Symp. 6, Bethesda.

Miller, T.J., L.B. Crowder, J.A. Rice, and E.A. Marschall
1988 Larval size and recruitment mechanisms in fishes: Toward a conceptual framework. Can. J. Fish. Aquat. Sci. 45:1657–1670.

Moser, H.G., and E.H. Ahlstrom
1978 Larvae and pelagic juveniles of blackgill rockfish, *Sebastes melanostomus*, taken in midwater trawls off southern California and Baja California. J. Fish. Res. Board Can. 35:981–996.

Moser, H.G., and G.W. Boehlert
1991 Ecology of pelagic larvae and juveniles of the genus *Sebastes*. Environ. Biol. Fishes 30:203–224.

Penney, R.W., and G.T. Evans
1985 Growth histories of larval redfish (*Sebastes* spp.) on an offshore Atlantic fishing bank determined by otolith increment analysis. Can. J. Fish. Aquat. Sci. 42:1452–1464.

PFMC (Pacific Fishery Management Council)
1989 Status of the Pacific coast groundfish fishery through 1989 and recommended acceptable biological catches for 1990. Pac. Fish. Manage. Counc., Portland, 299 p.

Reilly, C.A., T. Wyllie Echeverria, and S. Ralston
In prep. Interannual variation and overlap in the diets of pelagic juvenile rockfishes (Genus: *Sebastes*) off central California. Manuscript submitted to Fishery Bulletin.

Rothschild, B.J.
1986 Dynamics of marine fish populations. Harvard Univ. Press, Cambridge, 277 p.

Sissenwine, M.P.
1984 Why do fish populations vary? *In* May, R.M. (ed.), Exploitation of marine communities; Report of the Dahlem workshop on exploitation of marine communities, Berlin, April 1–6, 1984, p. 59–94. Springer-Verlag, Berlin.

Smith, R.L.
1968. Upwelling. Oceanogr. Mar. Biol. Annu. Rev. 6:11–46.

Snedecor, G.W., and W.G. Cochran
1967 Statistical methods, 6th ed. Iowa State Univ. Press, Ames, 593 p.

Thorrold, S.R.
1989 Estimating some early life history parameters in a tropical clupeid, *Herklotsichthys castelnaui*, from daily growth increments in otoliths. Fish. Bull., U.S. 87:73–83.

Walters, C.J.
1989 Value of short-term forecasts of recruitment variation for harvest management. Can. J. Fish. Aquat. Sci. 46: 1969–1976.

Wyllie Echeverria, T.
1987 Thirty-four species of California rockfishes: Maturity and seasonality of reproduction. Fish. Bull., U.S. 85:229–250.

Wyllie Echeverria, T., W.H. Lenarz, and C.A. Reilly
1990 Survey of the abundance and distribution of pelagic young-of-the-year rockfishes, *Sebastes*, off central California. Tech. Memo. NOAA-TM-NMFS-SWFC-147, Southwest Fish. Sci. Cent., La Jolla, 125 p.

Yoklavich, M.M., and G.W. Boehlert
1987 Daily growth increments in otoliths of juvenile black rockfish, *Sebastes melanops*: An evaluation of autoradiography as a new method of validation. Fish. Bull., U.S. 85:826–832.

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Uptake and utilization of ^{14}C-glycine by embryos of *Sebastes melanops*

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Synopsis

The ability of embryos of the viviparous scorpaenid *Sebastes melanops* to take up nutrients from an exogenous substrate was demonstrated by incubating embryos at various stages of development (18–30 days after fertilization) in ^{14}C-labeled glycine for 24 h. Uptake was highest for embryos at the latest stages (28–30 days) and increased at a linear rate during the incubation period. Nutrient uptake was not time dependent in embryos at the early stages (18–22 days). Nutrient utilization by *S. melanops* embryos was measured by the oxidation of ^{14}C-labeled glycine to $^{14}CO_2$. The amount of respired $^{14}CO_2$ by the oldest embryos increased significantly at a linear rate over the 24 h incubation period. There was no evidence of nutrient utilization by the youngest embryos. The developmental changes we observed in the uptake and utilization of exogenous glycine are supported by our previous findings that the oldest embryos have fully developed mouths and guts, and require additional nutrition from intraovarian sources at this stage of development.

Introduction

The extent of maternal-embryonic relationships in viviparous fishes has been thoroughly reviewed by Wourms et al. (1988). Internal fertilization and embryonic gestation are common to all viviparous fishes. Among the viviparous teleost fishes, an evolutionary trend has formed in the maternal-embryonic trophic relationship, ranging from primitive lecithotrophy, in which embryonic nutrition is supplied endogenously from yolk stored in the egg, to highly advanced forms of matrotrophy, in which a significant amount of energy is transferred via specialized trophic structures from the mother to the offspring during embryonic development.

Until recently, members of the viviparous genus *Sebastes* were considered lecithotrophic, depending solely upon energy from yolk reserves for embryonic development (Balon 1981, Wourms 1981). Although a systematic study of the maternal contribution to embryonic development has yet to be accomplished in this speciose group, it now has been suggested that embryos of black rockfish, *S. melanops* (Boehlert & Yoklavich 1984), kurosoi, *S. schlegeli* (Boehlert et al. 1986), and copper rockfish, *S. caurinus* (Dygert & Gunderson 1991) derive additional energy from a source other than yolk. Evidence for matrotrophy in these species includes a marked discrepancy between the energy available in the yolk and the amount catabolically expended by the gestating embryos. Additionally, ultrastructural studies of the hindgut of *Sebastes* embryos just before hatching indicate a functional gut and digestion of protein (Shimizu et al. 1991).

Amino acids, proteins and lipids are probable components of exogenous nutrition supplied to developing embryos of viviparous fishes. Uptake of proteins occurs in the trophotaeniae of embryonic goodeids (Lombardi & Wourms 1985), and absorption of amino acids has been demonstrated in embryonic poeciliids (Grove & Wourms 1982) and clinids (Veith 1979). This may be the case for *S. melanops* embryos, because total nitrogen levels remain constant while proteins decrease over development, indicative of supplemental nitrogenous nutrition (Boehlert & Yoklavich 1984). Degeneration of eggs and embryos during intraovarian development and maternal secretions from the ovarian epithelium are possible sources of histotrophe in *Sebastes* (Boehlert & Yoklavich 1984, Boehlert et al. 1986).

The objectives of the present study are (1) to demonstrate, through in vitro experiments with a radiolabeled amino acid, the direct uptake and use of nutrients from an exogenous substrate by *S. melanops* embryos at various stages of development, and (2) to attempt to identify the site of uptake in the embryos by autoradiography.

Sebastes melanops occupies shallow, coastal water from Baja California to the Aleutian Islands (Hart 1973). Females give birth typically from January through March (Laroche & Richardson 1980). The duration of gestation is 37 days at 10° C; hatching occurs about 5 days prior to parturition. Newly extruded, pelagic larvae of *S. melanops* are relatively small (notochord length = 4.5 mm), with little remaining yolk, yet have fully pigmented eyes, a functional mouth and gut and are ready to initiate feeding.

Materials and methods

Adult *S. melanops* were captured from November 1984 to January 1985 by hook and line in 15–30 m of water off Oregon and transported alive to Oregon State University's Hatfield Marine Science Center, Newport, Oregon. The fish were held in circular 700 l tanks (1.2 m diameter) with running seawater at ambient temperature (about 10° C). Prior to experimentation, females were catheterized, and developmental stages of their embryos were determined using criteria described in Yamada & Kusakari (1991). Three females (fish No. 18, 141 and 19), examined on 31 January 1985, were gravid; embryos from each female were assigned developmental stages 21, 22 and 28 respectively.

Experiments on nutrient uptake and utilization were conducted on 4 and 6 February 1985 in a thermally controlled room at 10° C. Embryos were removed from anesthetized (MS-222) females by gentle catheterization, staged and placed into Gilson respirometer flasks (15 ml capacity) containing 4 ml of fish saline (Forster & Hong 1958) that was isosmotic with ovarian fluid (342 mOsM kg^{-1}). The saline contained 0.495 μCi ml^{-1} of ^{14}C-glycine (New England Nuclear, lot No. 533-25). Four replicate flasks, each containing an average of 191 embryos (range = 119–324), were used for each female. A filter paper wick and 0.100 ml of 10% potassium hydroxide (KOH) were placed in the sidearm or center well of each flask to capture $^{14}CO_2$ respired from glycine utilization. The flasks were stoppered and gently shaken during experiments. A control flask with no embryos was used to determine blank values of $^{14}CO_2$ production.

One flask of embryos from each female was terminated at 2, 4, 8 and 24 h after embryos were introduced to the radiolabeled saline. The filter paper and KOH were transferred into a scintillation vial with 10 ml of Ready-Solv EP fluor (Beckman). The radiolabeled saline was removed, and the flask and embryos were rinsed twice with a larger volume of fresh, unlabeled saline to remove surface contamination of the label.

Three replicates of 20 embryos were removed from the unlabeled saline, placed on a glass fiber filter and blotted from underneath to remove excess saline. The filter and embryos were digested overnight at 60° C in a scintillation vial with 1.0 ml of tissue solubilizer (Beckman BTS). After cooling to room temperature and the addition of 0.1 ml glacial acetic acid to reduce chemiluminescence, the dissolved embryonic tissue was diluted with 10 ml of fluor, dark adapted and assayed for radioactivity in a Beckman LS 8000 liquid scintillation counter. Experimental controls included (1) embryos not exposed to labeled saline but handled identically to the radioactive ones, and (2) blank glass fiber filters wetted with the wash saline from an experimental flask.

Activity (counts per minute) was corrected for counting efficiency by developing a quench curve with standard, calibrated samples of ^{14}C treated similarly to experimental samples; counting efficiency averaged 86.5%. Corrected activity was expressed as disintegrations per minute (DPM); glycine uptake per embryo was calculated as (total DPM – control DPM) (20 embryos)$^{-1}$ (0.3873 × 10^{-6} μg glycine DPM^{-1}). Utilization of glycine was measured as (total $^{14}CO_2$ DPM – control DPM) (No. embryos)$^{-1}$.

Additional embryos from the flasks were prepared for autoradiography. They were embedded in histological resin (LR White), sectioned sagittally at 1 μm and affixed to microscope slides. The slides were dipped in Kodak NTB-2 nuclear track emulsion, thoroughly dried and exposed in light tight boxes for 2–21 days at room temperature. The autoradiographs were developed in Kodak D-19 developer for 2 min, fixed for 5 min in Kodak fixer, rinsed for 20 min and stained in hematoxylin and eosin. Sections of embryos were examined at 1000 × magnification for location of exposed silver grains.

Results

Sebastes melanops embryos were at developmental stages 24.5, 25 and 30 on 4 February (experiment 1); based on the stage duration (Boehlert & Yoklavich 1984), the time since fertilization was 18.1, 18.8 and 27.4 days respectively (Table 1). Embryos from the same females had progressed approximately one stage by 6 February (experiment 2). Glycine uptake was variable but positive in all experiments (Table 2). Competition for or depletion of ^{14}C-glycine in the substrate was unlikely, with an average of only 0.6% of the radioactivity removed (as evident from the combined activity in the embryonic tissue and CO_2 fractions). Values of glycine uptake in experiment 1 were significantly higher ($p < 0.01$) than in experiment 2 based on a three-way analysis of variance (ANOVA) testing for the effects of individual fish (i.e. stage of embryonic development), incubation time and experiment on glycine uptake, and post-hoc multiple comparisons. Uptake rates were significantly higher ($p < 0.01$) for the embryos from fish number 19, at stages 30 and 31 during experiment 1 and experiment 2 respectively. No significant difference was found in uptake rates between fish numbers 18 and 141, whose embryos were at similar developmental stages. The overall relationship of uptake with time was not significant ($p = 0.398$). To further test the relationship between incubation time and glycine uptake in embryos from different fish, the uptake values within experiments were standardized by fish (mean = 0, SD = 1), thereby allowing for the combination of data from both experiments. Correlation coefficients between incubation time and glycine uptake were significant ($p < 0.01$) only for the fish (No. 19) with embryos at the most advanced developmental stages, suggesting that glycine uptake increased with time only for these embryos (Fig. 1).

Glycine utilization was measured as $^{14}CO_2$ production, and these experiments suggested slightly different results. For embryos younger than developmental stage 30, subtraction of the control $^{14}CO_2$

Table 1. Developmental stages of *Sebastes melanops* embryos used for nutrient-uptake experiments at 10° C. Time since fertilization at each stage was estimated from Boehlert & Yoklavich (1984).

Developmental stage	Time since fertilization (days)	Stage characteristics
24.5 and 25	18.1 18.8	Eyes partially pigmented; gut formed; heart beats; pectoral fin buds
26	20.4	Liver development
30	27.4	Mouth formed and open; caudal fin rays; gut continuous and open; hindgut with amorphous material
31	29.3	Pre-hatching; peristaltic movement of gut

values resulted in negative mean estimates of $^{14}CO_2$ production (Table 3). In the experiments with embryos at the late stages, however, respired $^{14}CO_2$ increased significantly with time, indicating that these embryos metabolically used glycine (Fig. 2).

Absolute identification of a site of nutrient uptake in our study of *S. melanops* embryos remains problematic. Autoradiographs of embryonic tissue containing radioactive glycine and exposed for 2–21 days were largely negative; no visible image of reduced silver grains was produced systematically in association with areas of radioactivity. Some activity of carbon-14 was evident as isolated silver grains along the exterior surface of the epidermis in a few sections of the finfold in the nape and head regions of embryos at stage 25 following 24 h of incubation (Fig. 3). Although the nuclear emulsion (NTB2) is recommended to detect low-energy isotopes such as carbon-14 by light microscropy (Gahan 1972), the amount of radioactive glycine incorporated into a 1 μm section of tissue may be insufficient to produce a positive, discernible image within a reasonable exposure time. Because NTB2 exhibits a high efficiency level in detecting radiation, increased sensitivity is associated with a greater tendency for high background fog levels; consequently, only grain densities well above background can be identified as bonafide autoradiographs.

Table 2. Uptake of ^{14}C-glycine by embryos of *Sebastes melanops*. Values of glycine uptake are means of three replicates; values in parentheses are standard deviations.

Fish No.	Developmental stage	Time (h)	Glycine uptake ($\times 10^{-6}$ μg embryo^{-1})	
Experiment 1				
18	24.5	2	53.495	(36.167)
18	24.5	4	19.432	(2.496)
18	24.5	8	23.202	(2.845)
18	24.5	24	29.344	(6.228)
141	25	2	28.218	(5.835)
141	25	4	59.918	(30.534)
141	25	8	119.031	(71.149)
141	25	24	40.728	(8.593)
19	30	2	218.863	(134.482)
19	30	4	81.496	(62.033)
19	30	8	116.714	(89.571)
19	30	24	298.204	(332.064)
Experiment 2				
18	25.5	2	12.548	(1.317)
18	25.5	4	12.338	(1.889)
18	25.5	8	12.348	(2.072)
18	25.5	24	44.526	(4.816)
141	26	2	6.048	(1.059)
141	26	4	13.874	(2.027)
141	26	8	15.504	(8.363)
141	26	24	53.356	—
19	31	2	9.153	(0.846)
19	31	4	27.046	(7.356)
19	31	8	43.771	(36.190)
19	31	24	57.488	(5.039)

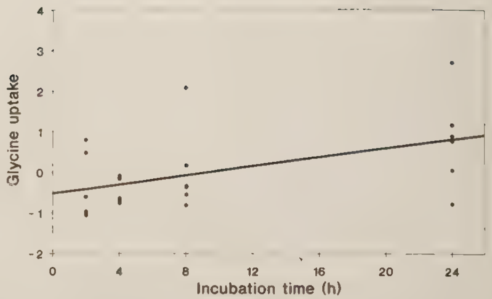

Fig. 1. Glycine uptake as a function of incubation time for developmental stages 30–31 in embryos from *Sebastes melanops* (fish No. 19). Data within each experiment were standardized (mean = 0, SD = 1) prior to analysis. The relationship (solid line) is described by the linear regression: Glycine uptake = − 0.533 + 0.056 (time); N = 24 and r = 0.506.

Discussion

Although our results do not cover a wide range of developmental stages, they suggest a fundamental difference between the *S. melanops* embryos at stages 24–26 and 30–31. Glycine uptake in embryos at the early stages was not significantly related to incubation time, and no glycine utilization was documented. Both uptake and utilization of glycine in embryos at the late stages, however, were time dependent (Fig. 1, 2). The most significant developmental event in the intervening stages is the opening of the mouth, which generally occurs near developmental stage 28 (Yamada & Kusakari 1991). Associated with this event, amorphous material has been noted in the hindgut lumen of *S.*

Table 3. Production of $^{14}CO_2$ (disintegrations per minute) by embryos of *Sebastes melanops*. Values are based on a single estimate per time period.

Fish No.	Time (h)	$^{14}CO_2$ production (DPM embryo^{-1})	
		Experiment 1	Experiment 2
18	2	– 0.761	–0.070
18	4	– 0.937	0.346
18	8	– 1.970	–0.898
18	24	– 1.639	–2.054
141	2	– 1.428	–0.355
141	4	– 0.344	–0.352
141	8	– 0.540	–0.056
141	24	– 3.704	–
19	2	0.622	1.595
19	4	1.336	2.209
19	8	0.219	3.323
19	24	14.336	8.455

schlegeli (Shimizu & Yamada 1980, Boehlert et al. 1986), *S. melanops* (Boehlert & Yoklavich 1984) and *S. caurinus* (Stahl-Johnson 1984) embryos at late stages.

Several structural and functional adaptations for nutrient transfer prior to opening of the mouth have developed in viviparous teleost embryos. Absorption of nutrients from embryotrophe takes place across the embryonic epidermis during early development and via the epithelium of fins and gut during later stages in some species of clinids (Veith 1980, Cornish & Veith 1986). More advanced absorptive structures include the trophotaeniae, which are extensions of the embryonic gut in goodeids (Turner 1937, Lombardi & Wourms 1985), and spatulate median fins in embiotocids (Webb & Brett 1972, Dobbs 1975). *Sebastes* embryos have no obvious structures for nutrient uptake or respiration. However, intracellular digestion of a nitrogenous-based histotrophe has been suggested from histological examination of the hindgut epithelium in late-stage embryos of *S. schlegeli* (Boehlert et al. 1986) and *S. melanops* (Boehlert & Yoklavich 1984). Evidence includes a hypertrophied hindgut epithelium with cells characterized by apical microvilli and numerous supranuclear, eosinophilic inclusions (Fig. 4a). Similar inclusions have been described in the hindgut epithelium of healthy, actively feeding larvae of marine fish (O'Connell 1976, Theilacker 1978). Such inclusions were less numerous or entirely absent from the epithelial cells in the hindgut of *Sebastes* embryos at the early stages (Fig. 4b). Ultrastructural examination of hindgut epithelium of *S. melanops* embryos at stage 28, following incubation in the protein-tracer horseradish peroxidase (HRP), demonstrated ac-

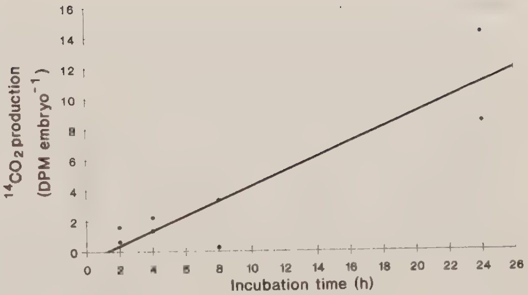

Fig. 2. Production of $^{14}CO_2$ as a function of incubation time by developmental stages 30–31 in embryos from *Sebastes melanops* (fish No. 19). Data from two experiments are combined. The relationship (solid line) is described by the linear regression: $^{14}CO_2$ production = $-0.580 + 0.483$ (time); $N = 8$ and $r = 0.909$.

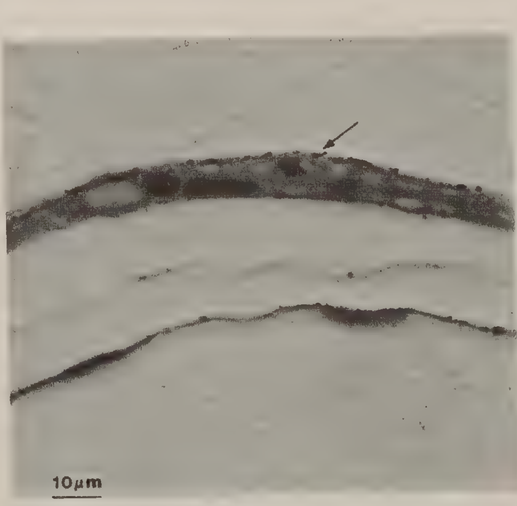

Fig. 3. Autoradiograph of a transverse histological section of dorsal finfold epidermis in the nape region of a *Sebastes melanops* embryo at stage 25 (about 19 days after fertilization). Note the black exposed grains on the surface of the epidermis (arrow).

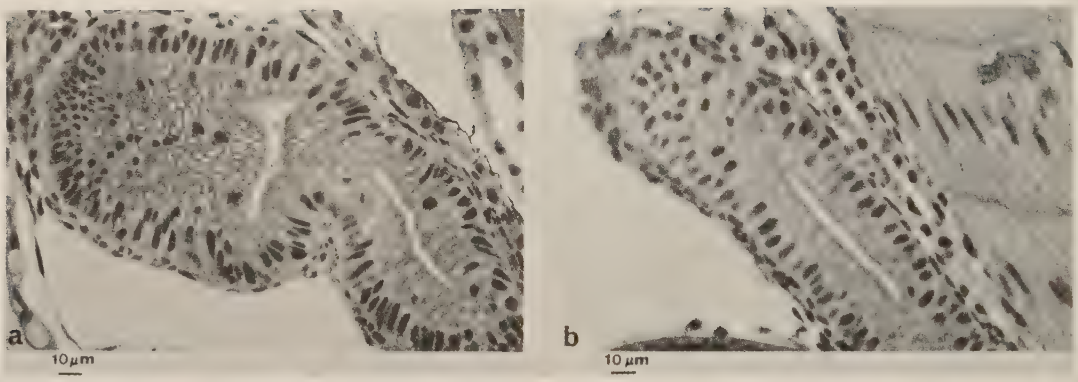

Fig. 4. Histological sections of hindgut tissue of embryos of *Sebastes melanops*: a – Cross section of the hindgut of an embryo at stage 30 (about 27 days post-fertilization). The expanded epithelium is characterized by intracellular, supranuclear, eosinophilic inclusions. b – Sagittal section of mid- and hindgut region dorsal to the yolk sac in an embryo at stage 25 (about 19 days post-fertilization).

tive uptake of high molecular weight substances (Shimizu et al. 1991).

The demonstrated uptake of glycine in embryos of *S. melanops* at the early stages is at odds with their lack of glycine utilization. Although certainly not definitive, the uncommon occurrence of exposed silver grains along the surface of the epidermis of embryos at the early stages suggests perhaps some of the radioactivity is due to superficial adsorption of the glycine and therefore remains metabolically unavailable. Alternatively, within the 24 h incubation period, nutrients possibly were being taken up but not metabolized appreciably by embryos at the early stages. Although the protein-tracer HRP generally was not incorporated into the epidermis of *S. melanops* embryos at stage 24 (Shimizu et al. 1990), a few outer epidermal cells contained inclusions of HRP and had well-developed apical microvilli; this suggests that some uptake of nutrients may occur at these sites in younger embryos.

A comparison of energy utilization by *S. melanops* embryos, based upon calorimetry and catabolism, indicated that a divergence between these estimates occurred at about developmental stage 28 and suggests that additional nutrition is required to continue development to parturition (Boehlert & Yoklavich 1984). This supports the developmental changes we have observed in both uptake and utilization of exogenous glycine by embryos at the late stages.

Acknowledgements

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References cited

Balon, E.K. 1981. Additions and amendments to the classification of reproductive styles in fishes. Env. Biol. Fish. 6: 377–389.

Boehlert, G.W., M. Kusakari, M. Shimizu & J. Yamada. 1986. Energetics during embryonic development in kurosoi, *Sebastes schlegeli* Hilgendorf. J. Exp. Mar. Biol. Ecol. 101: 239–256.

Boehlert, G.W. & M.M. Yoklavich. 1984. Reproduction, embryonic energetics, and the maternal-fetal relationship in the viviparous genus *Sebastes* (Pisces: Scorpaenidae). Biol. Bull. 167: 354–370.

Cornish, D.A. & W.J. Veith. 1986. Embryonic adaptations and nutrition in the viviparous teleost *Clinus dorsalis* (Perciformes: Clinidae). S. Afr. Tydskr. Dierk. 21: 79–84.

Dobbs, G.H. 1975. Scanning electron microscopy of intraovarian embryos of the viviparous teleost *Micrometrus minimus* (Gibbons), (Perciformes: Embiotocidae). J. Fish Biol. 7: 209–214.

Dygert, P.H. & D.R. Gunderson. 1991. Energy utilization by embryos during gestation in viviparous copper rockfish, *Sebastes caurinus*. Env. Biol. Fish. 30: 165–171.

Forster, R.P. & S.K. Hong. 1958. *In vitro* transport of dyes by isolated renal tubules of the flounder as disclosed by direct visualization: intracellular accumulation and transcellular movement. J. Cell. Comp. Physiol. 51: 259–272.

Gahan, P.B. (ed.). 1972. Autoradiography for biologists. Academic Press, London. 124 pp.

Grove, B.D. & J.P. Wourms. 1982. Embryonic nutrient absorption in the poeciliid *Heterandria formosa*. Amer. Zool. 22: 881.

Hart, J.L. 1973. Pacific fishes of Canada. Fish. Res. Board Can. Bull. 180: 1–740.

Laroche, W.A. & S.L. Richardson. 1980. Development and occurrence of larvae and juveniles of the rockfishes *Sebastes flavidus* and *Sebastes melanops* (Scorpaenidae) off Oregon. U.S. Fish. Bull. 77: 901–924.

Lombardi, J. & J.P. Wourms. 1985. The trophotaenial placenta of a viviparous goodeid fish. III: Protein uptake by trophotaeniae, the embryonic component. J. Exp. Zool. 236: 165–179.

O'Connell, C.P. 1976. Histological criteria for diagnosing the starving condition in early post yolk sac larvae of the northern anchovy, *Engraulis mordax* Girard. J. Exp. Mar. Biol. Ecol. 25: 285–312.

Shimizu, M., M. Kusakari, M.M. Yoklavich, G.W. Boehlert & J. Yamada. 1991. Ultrastructure of the epidermis and digestive tract in *Sebastes* embryos, with special reference to the uptake of exogenous nutrients. Env. Biol. Fish. 30: 155–163.

Shimizu, M. & J. Yamada. 1980. Ultrastructural aspects of yolk absorption in the vitelline syncytium of the embryonic rockfish, *Sebastes schlegeli*. Jap. J. Ichthyol. 27: 56–63.

Stahl-Johnson, K.L. 1984. Rearing and development of larval *Sebastes caurinus* (copper rockfish) and *S. auriculatus* (brown rockfish) from the northeastern Pacific. M.Sc. Thesis, University of Washington, Seattle. 218 pp.

Theilacker, G.H. 1978. Effect of starvation on the histological and morphological characteristics of jack mackerel, *Trachurus symmetricus*, larvae. U.S. Fish. Bull. 76: 403–414.

Turner, C.L. 1937. The trophotaeniae of the Goodeidae, a family of viviparous cyprinodont fishes. J. Morphol. 61: 495–523.

Veith, W.J. 1979. The chemical composition of the follicular fluid of the viviparous teleost *Clinus superciliosus*. Comp. Biochem. Physiol. 63A: 37–40.

Veith, W.J. 1980. Viviparity and embryonic adaptations in the teleost *Clinus superciliosus*. Can. J. Zool. 58: 1–12.

Webb, P.W. & J.R. Brett. 1972. Respiratory adaptations of prenatal young in the ovary of two species of viviparous seaperch, *Rhacochilus vacca* and *Embiotoca lateralis*. J. Fish. Res. Board Can. 29: 1525–1542.

Wourms, J.P. 1981. Viviparity: the maternal-fetal relationship in fishes. Amer. Zool. 21: 473–515.

Wourms, J.P., B.D. Grove & J. Lombardi. 1988. The maternal-embryonic relationship in viviparous fishes. pp. 1–135. *In:* W.S. Hoar & D.J. Randall (ed.) Fish Physiology, vol. 11 (part B). Academic Press, San Diego.

Yamada, J. & M. Kusakari. 1991. Staging and the time course of embryonic development in kurosoi, *Sebastes schlegeli*. Env. Biol. Fish. 30: 103–110.

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Temporal and Spatial Patterns in Abundance and Diversity of Fish Assemblages in Elkhorn Slough, California

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ABSTRACT: **Assemblages of ichthyofauna of shallow inshore habitats along California's central coast are described in terms of species composition, abundance, and life-style categories. A total of 22,334 fishes from 65 species and 27 families was collected with otter trawls at six sites in the main channel and tidal creeks of Elkhorn Slough, a tidal embayment and seasonal estuary, and two nearshore ocean stations in Monterey Bay during 44 months between August 1974 and June 1980. Greater than 90% of the catch comprised 10 species. The four dominant species, *Cymatogaster aggregata, Leptocottus armatus, Phanerodon furcatus,* and *Embiotoca jacksoni*, occurred during most or all seasons and were classified as residents or partial residents. Several abundant species were marine immigrants that seasonally use the slough as spawning and nursery grounds; this resulted in higher abundance and species richness during summer. Species collected during winter largely were slough residents. Species composition and richness varied with distance from the slough entrance. The ocean assemblage was most different, and its similarity to other stations decreased progressively with distance inland and into the tidal creeks. During our study, 5,074 fishes were collected by beach seine in Bennett Slough, a remote shallow marsh basin adjacent to the entrance of Elkhorn Slough. Species richness was relatively low and three euryhaline species accounted for >80% of the total catch. The species assemblage was most similar to those at the tidal creek and most shallow stations of Elkhorn Slough. Resident species numerically dominated assemblages in Bennett Slough and the most inland areas of Elkhorn Slough. The high relative abundance of marine-related fishes (classified as marine, marine immigrant, and partial resident) entering Elkhorn Slough early in life or as spawning adults indicates the importance of this habitat to nearshore fish assemblages.**

Introduction

Shallow bays and estuaries are recognized worldwide as productive habitats used by a variety of fishes for reproduction, feeding, and shelter (Odum and Heald 1975; Dando 1984; Day and Yanez-Arancibia 1985, among others). These systems function as important nursery grounds for larval and juvenile stages of many marine fishes, potentially enhancing their early growth and survival (Allen 1982; Rosenberg 1982; Weinstein 1985). This nursery function often has been discussed in terms of the estuarine dependence of marine species. More broadly, estuarine dependence includes any species using estuaries as essential habitat during any life history stage (Blaber et al. 1989). Those species regularly entering estuaries to spawn or feed, as well as those completing their entire life cycle in the area, also can be considered to be dependent on estuarine systems.

Because most species are not dependent entirely on estuaries and are found also in adjacent coastal environments, Lenanton and Potter (1987) suggested the term "estuarine opportunism." Although difficult to evaluate because it requires seasonal sampling over several years in all major habitats of the estuary and adjacent marine area, the benefits derived by opportunistic members of the estuarine fish assemblage would be a measure of the interaction between estuarine and coastal marine environments (Darnell and Soniat 1979; Weinstein 1981). Identifying this inshore-offshore relationship is important to maintaining all coastal resources.

The functional relationship between estuaries and fish communities has been studied widely along the east coast of the United States, particularly in expansive tidal marshes (Shenker and Dean 1979;

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Weinstein 1979; Bozeman and Dean 1980). Although estuaries represent only 10–25% of the west coast, compared to 80–90% of the Atlantic and Gulf of Mexico coasts (Day and Yanez-Arancibia 1985), they have been identified as important nursery and spawning areas for some commercially valuable marine fishes (Pearcy and Myers 1974; Krygier and Pearcy 1986; McGowan 1986; Gunderson et al. 1990). Bays and estuaries of California, in particular, are few in number and size; their total area is less than 15% that of Chesapeake Bay (Horn and Allen 1976). In addition, more than 75% of California's coastal wetlands have been lost or degraded through pollution, diking, and filling (Onuf et al. 1978). Nonetheless, unique assemblages of fishes using those remaining coastal systems contribute to California's nearshore marine resources (Allen 1982; Horn and Allen 1985).

Fish assemblages of Elkhorn Slough, a primarily marine-influenced wetland habitat on the central California coast, have been studied since the mid-1970s by faculty and graduate students of Moss Landing Marine Laboratories (California State University system). These investigations provide valuable information on life histories, abundance, and distribution of fishes throughout this system, including tidal creeks and adjacent Bennett Slough and marine coastal habitats (Ambrose 1976; Appiah 1977; Cailliet et al. 1977; Antrim 1981; Barry and Cailliet 1981; Yoklavich 1982; Barry 1983). Further interest has been stimulated by the recent designation of Elkhorn Slough as a member of the National Estuarine Research Reserve System and as the site of marsh restoration projects. Using data that were collected regularly during four years, the objectives of the present study were (1) to assess seasonal and spatial changes in species composition, abundance, and habitat associations of fish assemblages in Elkhorn Slough; and (2) to evaluate the interaction between fish assemblages in the slough and those in adjacent nearshore ocean habitat, especially in terms of "slough dependence or opportunism." This study provides baseline information prerequisite to long-term monitoring of fish assemblages in Elkhorn Slough, their response to potential environmental changes (both naturally and human-induced), and their contribution to the nearshore fishery resources of Monterey Bay.

Methods

STUDY AREA

Elkhorn Slough (36°48′N, 121°47′W) is a shallow, tidal embayment and seasonal estuary at the head of the Monterey submarine canyon. It has an axial length of about 10 km and a relatively small drainage basin of 585 km² (Fig. 1; Browning 1972). During our study, water depth of the main channel below mean lower low water (MLLW) ranged from about 5 m at the slough entrance to less than 2 m at the most inland station; average width of the main channel narrowed from 100 m at the entrance to 15 m furthest inland (Smith 1973; Broenkow 1977). The main channel is bordered by extensive mudflats (about 170 ha are exposed at MLLW) and is intersected by a network of tidal creeks that meander through adjacent salt marshes (about 583 ha comprised predominantly of pickleweed [*Salicornia virginica*]).

Our study area included several sites along the main channel of the slough, from the entrance to Hudson's Landing (Fig. 1). In addition, we sampled Long Canyon, a tidal creek that is 1–1.5 km long, 5–10 m wide and 2 m deep at its intersection with the main channel (about 4 km east of Moss Landing Harbor entrance), and receives freshwater runoff from the adjacent watershed. We also sampled Rubis Creek (Fig. 1), which intersects the main channel across from Long Canyon Creek and is about the same width and depth but receives little freshwater runoff.

Semidiurnal tides with a mean tidal range of 1.1 m result in well-mixed water in two environmentally distinct zones of the slough (Broenkow 1977). The area above the mean tidal prism, which is about 4.8 km inland, has a water residence time in excess of 300 d. Salinity in this region of the slough varied seasonally with evaporation, precipitation, and runoff, and ranged from 17‰ in March to 37‰ in June. Water temperature ranged from 12°C to 26°C. Water west of the tidal prism (about 75% of the mean high water volume) is exchanged daily and reflects nearshore ocean conditions, with cooler temperatures (12–18°C) and more constant salinity (29–34‰).

Our study also included Bennett Slough, a shallow (0.3–1.8 m) semi-enclosed embayment that is connected to Elkhorn Slough via a culvert (0.6 m diameter) at the north end of Moss Landing Harbor (Fig. 1). Substratum was soft mud, mean water temperature ranged from 10.5°C in January to 21.5°C in June, and mean salinity was constant, varying from 30‰ in February to 33‰ in June (Appiah 1977).

SAMPLING METHODS

Fishes were collected at least monthly from August 1974 to June 1976 at three locations in the main channel of Elkhorn Slough, approximately 0.6 km (the bridge station), 3.1 km (the dairy station), and 6.0 km (the Kirby Park station) inland, and at two locations on the sandy shelf (water depth = 5–10 m) north and south of the Moss Landing Harbor entrance (the ocean station; Fig. 1). At least monthly collections were taken in the main channel at the Hudson's Landing station (about 10 km inland from the entrance of the slough) from January 1979 to June 1980 and in two tidal creeks (the Long Canyon and Rubis Creek stations) from October 1978 to June 1980. Fishes were collected about monthly in Bennett Slough from August 1974 to August 1976.

Collections in the main channel were taken with a 4.8 m otter trawl (3.8 cm stretch-mesh body with 1.3 cm codend liner) towed at 3–4 knots behind a 5 m Boston Whaler for 5 min or 10 min into the current at flood tide. In tidal creeks, this gear was towed at 1.5–2.5 knots between fixed markers during daylight. Catch data from otter trawls were standardized to number of fish per 10-min tow for seasonal and spatial comparisons. Plots of cumulative number of species against a randomly pooled number of samples (collected at the dairy station from May to October, 1975 and 1976, a period of high species richness) indicated that six tows were adequate to describe spatial and temporal patterns in species composition and abundance in the slough environment (Cailliet et al. 1977).

Collections in Bennett Slough were taken with a beach seine (15.2 m long with 0.6 cm and 1.3 cm meshes) fished along shore for an average of 30 m per haul to a maximum depth of 1.3 m. In areas of the tidal creeks that were <1.5 m in depth, fishes were collected periodically with beach seines and channel nets made of 3–6 mm² mesh nylon, similar to those of Bozeman and Dean (1980). At high-high slack tide, 8–10 channel nets were placed across creeks and tributaries, lead line forced into the sediment and ends secured above the channel bank. Fishes were collected as tidal level dropped and nets were exposed. Catch data from beach seines and channel nets were expressed as number of fish per haul.

Fishes were identified, counted, measured to the nearest mm in standard length (SL), and either released or preserved with 10% formalin.

Abundance (mean number of fishes per species per tow), species richness (mean number of species per tow), and dominance ($D = \Sigma P_i^2$, where P_i is the proportional abundance of species i per tow) were evaluated by location for each season. The index of dominance measures unevenness of species abundance within an assemblage, gives relatively little weight to rare species, and ranges from $1 \times s^{-1}$ (where s = total number of species) to 1 (total dominance by one species). Seasons were defined as fall (August, September, October), winter (November, December, January), spring (February, March, April), and summer (May, June, July). These groupings approximated the climatic seasonality of the study area in terms of rainfall, air and water temperatures, and salinity (Broenkow 1977).

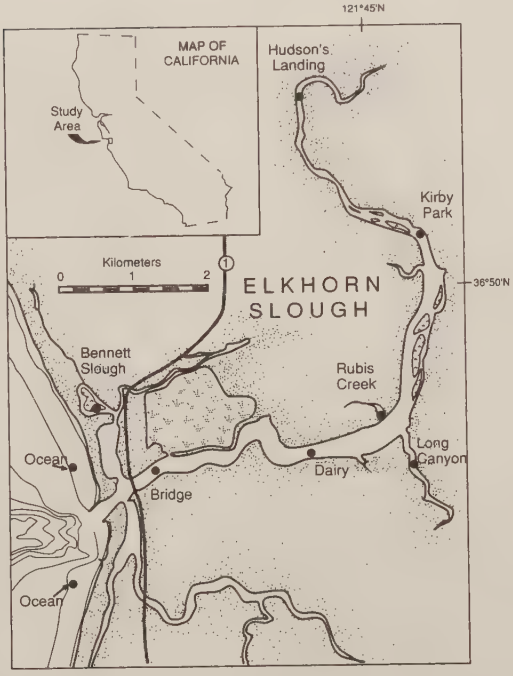

Fig. 1. Fish sampling locations (●) in Elkhorn and Bennett sloughs, California, and the adjacent nearshore ocean.

Species composition was compared between stations using the percentage similarity index (PSI; Krebs 1989):

$$\mathrm{PSI} = \sum \mathrm{minimum}(p_{1i}, p_{2i})$$

where PSI is the sum of the smallest percentage by number (p_{1i} and p_{2i}) of each pair of species i from stations 1 and 2, respectively. This index ranges from zero (no similarity) to 1.00 (identical species arrays). In the present study, PSI values greater than 0.60 were interpreted as significant, based on level of significance of product-moment correlation coefficient relative to PSI's (Cailliet and Barry 1978).

Each species was categorized (modified from Lenanton and Potter 1987; Loneragan et al. 1989) as either (1) a slough resident (R; spawns and completes entire life cycle in the slough); (2) a partial resident (PR; primarily lives in the slough, seasonally or ontogenetically moves to the ocean, and returns to reproduce in the slough); (3) marine immigrant (MI; primarily lives in the ocean and

TABLE 1. Relative abundance (%), mean number per 10-min tow (n), standard error (in parentheses), and life style (M = marine, MI = marine immigrant, R = slough resident, PR = partial resident, and F = freshwater) of fish species caught in otter trawls at six locations in Elkhorn Slough and at two nearshore ocean stations. Only those species representing >0.1% overall abundance are included. Overall abundance and rank are indicated. Dash (—) indicates species was not collected.

	Ocean		Bridge		Dairy	
Taxon	n	%	n	%	n	%
Amphistichus argenteus (M)	0.57 (0.27)	4.6	—	—	—	—
Atherinops affinis (PR)	—	—	1.14 (1.14)	0.5	0.02 (0.02)	<0.1
Atherinopsis californiensis (PR)	—	—	0.03 (0.03)	<0.1	0.06 (0.05)	0.1
Citharichthys stigmaeus (MI)	2.74 (0.55)	21.9	21.54 (6.66)	10.3	2.92 (0.92)	4.4
Clevelandia ios (R)	—	—	0.03 (0.03)	<0.1	—	—
Clupea pallasii (MI)	—	—	—	—	1.67 (1.61)	2.5
Cymatogaster aggregata (PR)	0.46 (0.32)	3.7	90.94 (69.10)	43.4	19.06 (4.69)	28.8
Damalichthys vacca (MI)	0.08 (0.06)	0.6	1.77 (0.55)	0.8	1.27 (0.35)	1.9
Dorosoma petenense (F)	—	—	—	—	—	—
Embiotoca jacksoni (R)	0.01 (0.01)	0.1	30.49 (7.02)	14.6	8.88 (2.73)	13.4
Engraulis mordax (MI)	—	—	0.66 (0.66)	0.3	0.10 (0.07)	0.2
Gobiidae	—	—	—	—	—	—
Hyperprosopon anale (M)	1.76 (0.57)	14.1	—	—	—	—
Hyperprosopon argenteum (MI)	0.07 (0.04)	0.6	1.63 (0.77)	0.8	0.86 (0.32)	1.3
Hypsopsetta guttulata (MI)	0.04 (0.02)	0.3	—	—	0.08 (0.05)	0.1
Lepidogobius lepidus (R)	—	—	0.17 (0.12)	0.1	0.06 (0.05)	0.1
Leptocottus armatus (R)	0.03 (0.03)	0.2	2.06 (0.96)	1.0	1.57 (0.50)	2.4
Micrometrus minimus (M)	0.01 (0.01)	0.1	1.17 (0.40)	0.6	0.37 (0.29)	0.6
Morone saxatilis (F)	—	—	—	—	—	—
Mustelus californicus (M)	—	—	—	—	—	—
Myliobatis californica (PR)	0.01 (0.01)	0.1	0.14 (0.06)	0.1	0.14 (0.05)	0.2
Neoclinus uninotatus (M)	—	—	0.40 (0.29)	0.2	—	—
Ophiodon elongatus (M)	0.22 (0.10)	1.8	0.34 (0.15)	0.2	0.02 (0.02)	<0.1
Paralichthys californicus (MI)	0.01 (0.01)	0.1	0.03 (0.03)	<0.1	—	—
Parophrys vetulus (MI)	0.53 (0.14)	4.2	7.14 (2.61)	3.4	2.63 (0.88)	4.0
Phanerodon furcatus (PR)	0.58 (0.20)	4.6	34.80 (8.17)	16.6	18.78 (4.63)	28.4
Platichthys stellatus (MI)	0.64 (0.13)	5.1	9.36 (1.09)	4.5	2.59 (0.41)	3.9
Pleuronichthys decurrens (M)	1.08 (0.68)	8.6	0.23 (0.12)	0.1	0.06 (0.03)	0.1
Porichthys notatus (MI)	—	—	0.29 (0.23)	0.1	0.61 (0.35)	0.9
Psettichthys melanostictus (M)	2.37 (0.55)	19.0	—	—	—	—

TABLE 1. Continued.

Kirby Park		Hudson's Landing		Long Canyon		Rubis Creek		Overall		
n	%	n	%	n	%	n	%	n	%	Rank
—	—	—	—	—	—	—	—	0.12	0.2	24
0.20 (0.13)	0.3	0.42 (0.36)	0.4	0.56 (0.21)	4.9	0.03 (0.03)	0.1	0.28	0.4	20
0.16 (0.09)	0.2	—	—	—	—	0.06 (0.04)	0.2	0.04	0.1	31
0.04 (0.03)	0.1	0.03 (0.19)	<0.1	0.03 (0.03)	0.3	0.10 (0.09)	0.3	3.14	5.0	6
—	—	0.33 (0.14)	0.3	0.43 (0.35)	3.7	0.68 (0.10)	1.8	0.20	0.3	22
0.80 (0.34)	1.0	15.23 (6.21)	15.0	0.19 (0.11)	1.7	1.47 (0.89)	3.8	2.46	3.9	8
41.71 (8.94)	53.7	1.58 (0.46)	1.6	0.34 (0.16)	3.0	5.98 (2.49)	15.5	18.54	29.4	1
0.31 (0.10)	0.4	—	—	—	—	0.32 (0.14)	0.8	0.46	0.7	11
0.59 (0.57)	0.8	0.40 (0.23)	0.4	—	—	0.03 (0.03)	0.1	0.14	0.2	24
2.16 (0.99)	2.8	—	—	0.43 (0.16)	3.7	2.97 (0.65)	7.7	5.01	8.0	4
3.61 (2.06)	4.6	18.65 (6.45)	18.3	0.22 (0.16)	1.9	3.55 (2.03)	9.2	3.42	5.4	5
—	—	0.08 (0.06)	0.1	0.19 (0.16)	1.7	0.10 (0.05)	0.3	0.05	0.1	31
—	—	—	—	—	—	—	—	0.38	0.6	13
0.27 (0.15)	0.3	0.03 (0.19)	<0.1	—	—	0.13 (0.08)	0.3	0.35	0.6	13
0.06 (0.03)	0.1	0.03 (0.19)	<0.1	0.06 (0.06)	0.5	0.03 (0.03)	0.1	0.05	0.1	31
0.47 (0.37)	0.6	—	—	0.03 (0.03)	0.3	—	—	0.09	0.1	31
10.20 (5.48)	13.1	58.67 (14.28)	57.6	5.89 (1.79)	51.2	15.87 (5.24)	41.1	12.20	19.4	2
—	—	—	—	—	—	0.16 (0.14)	0.4	0.19	0.3	22
—	—	0.66 (0.30)	0.6	—	—	—	—	0.08	0.1	31
0.02 (0.02)	<0.1	0.31 (0.18)	0.3	—	—	0.03 (0.03)	0.1	0.05	0.1	31
0.76 (0.25)	1.0	0.53 (0.35)	0.5	0.25 (0.14)	2.2	0.74 (0.44)	1.9	0.35	0.6	13
—	—	—	—	—	—	—	—	0.04	0.1	31
—	—	—	—	—	—	0.03 (0.03)	0.1	0.09	0.1	31
0.02 (0.02)	<0.1	0.82 (0.21)	0.8	0.19 (0.07)	1.7	1.14 (0.36)	3.0	0.30	0.5	18
8.33 (4.81)	10.7	0.75 (0.30)	0.7	—	—	0.74 (0.44)	1.9	2.53	4.0	7
1.73 (0.34)	2.2	—	—	0.19 (0.08)	1.7	0.52 (0.20)	1.3	6.49	10.3	3
4.57 (0.95)	5.9	2.10 (0.79)	2.1	0.68 (0.18)	5.9	0.43 (0.15)	1.1	2.47	3.9	8
—	—	—	—	—	—	—	—	0.26	0.4	20
0.88 (0.74)	1.1	0.26 (0.12)	0.3	—	—	0.13 (0.08)	0.3	0.29	0.5	18
—	—	—	—	—	—	—	—	0.51	0.8	10

TABLE 1. Continued.

Taxon	Ocean		Bridge		Dairy	
	n	%	n	%	n	%
Rhacochilus toxotes (M)	0.01 (0.01)	0.1	0.80 (0.48)	0.4	0.10 (0.04)	0.2
Scorpaenichthys marmoratus (MI)	0.07 (0.03)	0.6	3.71 (1.50)	1.8	0.55 (0.20)	0.8
Sebastes spp.	0.05 (0.03)	0.4	0.34 (0.23)	0.2	0.20 (0.15)	0.3
Sebastes auriculatus (M)	—	—	1.26 (0.59)	0.6	1.67 (0.76)	2.5
Sebastes mystinus (M)	0.07 (0.04)	0.6	0.60 (0.20)	0.3	0.53 (0.22)	0.8
Sebastes paucispinis (M)	0.08 (0.06)	0.6	0.20 (1.02)	0.1	0.41 (0.29)	0.6
Seriphus politus (MI)	—	—	—	—	—	—
Spirinchus starksi (M)	0.45 (0.38)	3.6	0.03 (0.03)	<0.1	—	—
Symphurus atricauda (MI)	—	—	0.09 (0.06)	<0.1	—	—
Syngnathus leptorhynchus (R)	0.09 (0.04)	0.7	0.17 (0.10)	0.1	0.04 (0.03)	0.1
Triakis semifasciata (PR)	—	—	0.06 (0.06)	<0.1	0.16 (0.11)	0.2
Urolophus halleri (M)	—	—	—	—	0.16 (0.08)	0.2

regularly enters the slough at some stage of life to feed, reproduce, or use the area as a nursery); (4) marine (M; coastal species rarely or never found in Elkhorn Slough); or (5) freshwater (F; primarily lives and reproduces in freshwater, but found rarely in the most inland area of the slough). Members of the resident and partial resident categories potentially can spawn and complete their life cycle outside the slough environment. Studies on the ichthyoplankton of Elkhorn Slough (Wang 1981; Yoklavich et al. 1992) and life histories of fishes in West Coast estuaries (NOAA 1990) were used to classify some species. The relative contribution made by number of individuals and number of species in each category to the fish assemblage of each slough region was evaluated. Regions were defined as upper slough and tidal creeks (Hudson's Landing, Long Canyon, and Rubis Creek stations), middle slough (Kirby Park station), lower slough (dairy and bridge stations), and Bennett Slough.

Results

A total of 22,334 fishes, representing 65 species from 27 families, was collected in 355 otter trawl tows at six stations in the main channel and tidal creeks of Elkhorn Slough and two nearshore ocean stations during 44 months between August 1974 and June 1980 (Table 1). Ten species accounted for >90% of all fishes taken in trawls throughout the study; relative abundance of these species ranged from 0.8% for *Psettichthys melanostictus* (sandsole), occurring only at the ocean station, to 29.4% for *Cymatogaster aggregata* (shiner surfperch), which was abundant at all stations.

The highest abundance and species richness occurred at the bridge station, where a mean density of 209 fish per 10-min tow and 37 species were collected in 35 tows (Table 2). The relatively high standard error (SE = 82.4) is largely due to 1,208 *C. aggregata* from a single collection during an intense episode of red tide. The large number of individuals and species likely reflects increased diversity of available habitat at the bridge station, including submerged rocks and pier pilings. Species more typical of rocky coastal marine habitats were collected in low numbers at the bridge station, including *Artedius harringtoni* (scalyhead sculpin), *Coryphopterus nicholsii* (blackeye goby), *Hexagrammos decagrammos* (kelp greenling), *Hypsurus caryi* (rainbow surfperch), *Neoclinus uninotatus* (onespot fringehead), *Ophiodon elongatus* (lingcod), *Scorpaenichthys marmoratus* (cabezon), and juvenile *Sebastes*, especially *S. auriculatus* (brown rockfish), *S. mystinus* (blue rockfish), *S. paucispinis* (bocaccio), and *S. rastrelliger* (grass rockfish; see Cailliet et al. [1977] for the abundance of less common species).

The ocean station and tidal creeks (Long Canyon and Rubis Creek stations) consistently had the lowest mean densities (12.5, 11.5, and 38.7 fish per 10-min tow, respectively, Table 2). The other three stations (i.e., dairy, Kirby Park, and Hudson's Landing) along the main channel were interme-

TABLE 1. Continued.

Kirby Park		Hudson's Landing		Long Canyon		Rubis Creek		Overall		
n	%	n	%	n	%	n	%	n	%	Rank
—	—	—	—	—	—	—	—	0.10	0.2	24
0.10 (0.05)	0.1	—	—	—	—	—	—	0.47	0.7	11
—	—	—	—	—	—	0.06 (0.09)	0.2	0.08	0.1	31
0.04 (0.04)	0.1	—	—	—	—	0.23 (0.12)	0.6	0.39	0.6	13
—	—	—	—	—	—	—	—	0.15	0.2	24
—	—	—	—	—	—	—	—	0.09	0.1	31
0.20 (0.13)	0.3	0.03 (0.19)	<0.1	1.09 (1.08)	9.5	0.09 (0.05)	0.2	0.06	0.1	31
—	—	—	—	—	—	—	—	0.10	0.2	24
—	—	0.22 (0.15)	0.2	0.12 (0.10)	1.0	0.60 (0.26)	1.6	0.14	0.2	24
—	—	—	—	—	—	0.58 (0.20)	1.5	0.12	0.2	24
0.27 (0.11)	0.3	0.29 (0.18)	0.3	0.43 (0.22)	3.7	1.55 (0.38)	4.0	0.36	0.6	13
0.14 (0.09)	0.2	—	—	—	—	—	—	0.04	0.1	31

diate in fish abundance. Species richness was highest at the three stations closest to the entrance of the slough (i.e., ocean, bridge, and dairy) and at the Rubis Creek station; overall dominance indices were lowest at these stations (Table 2).

Species composition of otter trawl catches was most similar between the bridge station and the other two stations in the main channel of the lower and middle region of Elkhorn Slough (i.e., dairy and Kirby Park, Table 3), largely because of the numerically dominant *C. aggregata* and other surfperch species. Fish assemblages at the most shallow inland station of the main channel (Hudson's Landing) and at the tidal creek stations (Rubis Creek and Long Canyon) were more similar to each other than to assemblages at any other station in the main channel. Species composition was most unique at the ocean station and similarity (PSI) to the other stations decreased progressively with distance inland and into the tidal creeks.

Dominant species at each site varied with distance inland (Table 4). Of the eight most abundant species taken at the ocean station, four were nonestuarine species not collected at any slough station, and representing nearly 50% of the total abundance at this station. Two abundant species were restricted to the ocean, bridge, and dairy stations. Notably, *Citharichthys stigmaeus* (speckled sanddab), the dominant species at the ocean station, and *Phanerodon furcatus* (white surfperch) were much less abundant east of the dairy station. *Cymatogaster aggregata* was numerically dominant at lower and middle slough stations of the main channel and in Rubis Creek. *Leptocottus armatus* (staghorn sculpin), a euryhaline cottid, was highest in abundance at stations furthest inland, and was the dominant spe-

TABLE 2. Summary of diversity, dominance, and abundance of fishes captured with otter trawls at six stations in Elkhorn Slough and at two nearshore ocean stations.

	Ocean	Bridge	Dairy	Kirby Park	Hudson's Landing	Long Canyon	Rubis Creek	Overall
Number of species	34	37	37	26	24	20	32	65
Dominance index	0.12	0.26	0.19	0.32	0.37	0.29	0.22	
Total number[a]	950	7,326	3,244	3,807	4,479	596	1,933	22,334
Mean number tow^{-1} (SE)	12.5 (1.6)	209.3 (82.4)	66.2 (2.0)	77.7 (15.3)	101.8 (21.8)	11.5 (1.7)	38.7 (9.6)	63.0
Number of tows	76	35	49	49	44	52	50	355

[a] Adjusted to 10-min tows.

TABLE 3. Comparison of fish species composition in otter trawl collections from six stations in Elkhorn Slough and two adjacent ocean stations based on percentage similarity index (PSI). Comparisons with the fish assemblage from beach seine collections in Bennett Slough also are indicated.

	Bridge	Dairy	Kirby Park	Hudson's Landing	Rubis Creek	Long Canyon	Bennett Slough
Ocean	0.30	0.25	0.17	0.05	0.11	0.11	0.08
Bridge	—	0.77	0.60	0.07	0.32	0.16	0.12
Dairy	—	—	0.48	0.11	0.36	0.18	0.14
Kirby Park	—	—	—	0.27	0.45	0.32	0.28
Hudson's Landing	—	—	—	—	0.61	0.62	0.30
Rubis Creek	—	—	—	—	—	0.66	0.35
Long Canyon	—	—	—	—	—	—	0.42

cies in trawls at the Hudson's Landing and tidal creek stations. *Engraulis mordax* (northern anchovy) and *Clupea pallasii* (Pacific herring) also were numerically dominant in otter trawls at the shallow inland stations.

For beach seine and channel net collections from the smallest tidal creeks (Table 5), overall species richness was only 16 (<10 species in the shallowest creeks) and dominance was higher (0.45–0.60) than in the main channel. Dominance indices increased because of the high relative abundance of juvenile *Atherinops affinis* (topsmelt, 62.7%). *Clevelandia ios* (arrow goby) and *E. mordax* also were relatively abundant (12.1% and 11.6%, respectively) in beach seine and channel net collections from the upper marshes.

Seasonal variation in fish abundance was high, with a noticeable depression in mean catch rate during the winter and early spring at most stations (Fig. 2). The exceptionally high peak in abundance at the bridge station during winter 1978 was caused by one large catch of *C. aggregata*. Peak abundance occurred in summer at most stations throughout the slough. Mean species richness per tow also decreased during winter (Fig. 3). Species collected in winter largely were slough residents (see Cailliet et al. [1977] and Barry [1983] for monthly species-specific catch rates). Seasonal patterns in mean dominance indices generally were opposite those in abundance and species richness, with peaks in winter and early spring months (Fig. 3). Trends in dominance were most apparent at the ocean station and lower slough stations (i.e., bridge and dairy) in the main channel.

During spring and summer, most species were present as juveniles, while some were collected in low numbers as reproductively active adults, including *C. pallasii, C. aggregata, Embiotoca jacksoni* (black surfperch), *Triakis semifasciata* (leopard shark), and *Myliobatis californica* (bat ray). Juvenile fishes contributed to the increase in abundance and species richness during this period, and many of

TABLE 4. Relative abundance (%) of dominant species totaling 80% (or greater) of the fishes collected in Elkhorn and Bennett sloughs and at adjacent nearshore ocean stations. See legend of Table 1 for coded life-style categories (in parentheses).

Species	Ocean	Bridge	Dairy	Kirby Park	Hudson's Landing	Long Canyon	Rubis Creek	Bennett Slough
Psettichthys melanostictus (M)	19.0							
Hyperprosopon anale (M)	14.1							
Pleuronichthys decurrens (M)	8.6							
Amphistichus argenteus (M)	4.6							
Citharichthys stigmaeus (MI)	21.9	10.3	4.4					
Phanerodon furcatus (PR)	4.6	16.6	28.4					
Parophrys vetulus (MI)	4.2		4.0	10.7				
Platichthys stellatus (MI)	5.1		3.9	5.9		5.9		22.0
Cymatogaster aggregata (PR)		43.4	28.8	53.7			15.5	
Embiotoca jacksoni (R)		14.6	13.4			3.7	7.7	
Leptocottus armatus (R)				13.1	57.6	51.2	41.1	23.7
Engraulis mordax (MI)					18.3		9.2	
Clupea pallasii (MI)					15.0		3.8	
Seriphus politus (MI)						9.5		
Atherinops affinis (PR)						4.9		
Clevelandia ios (R)						3.7		34.9
Triakis semifasciata (PR)						3.7	4.0	
Total (%)	82.1	84.9	82.9	83.4	90.9	82.6	81.3	80.6
Number of dominant species	8	4	6	4	3	7	6	3

TABLE 5. Number (Number = mean per sample and Percent = relative abundance) of fishes caught in beach seines in Bennett Slough from August 1974 to August 1976, and in beach seines and channel nets at the most shallow stations of Elkhorn Slough (i.e., Long Canyon, Rubis Creek, and Hudson's Landing) from October 1978 to June 1980. See legend of Table 1 for coded life-style categories (in parentheses).

Taxon	Bennett Slough		Elkhorn Slough	
	Number	Percent	Number	Percent
Acanthogobius flavimanus (R)	0.3	0.4	0.7	1.1
Atherinops affinis (PR)	1.5	2.6	38.9	62.7
Atherinopsis californiensis (PR)	0.6	1.1	—	—
Clevelandia ios (R)	20.6	34.9	7.5	12.1
Clupea pallasii (MI)	0.6	1.0	—	—
Cottus asper (F)	<0.1	<0.1	—	—
Cymatogaster aggregata (PR)	1.0	1.7	<0.1	0.1
Embiotoca jacksoni (R)	1.7	2.8	0.2	0.3
Engraulis mordax (MI)	0.2	0.4	7.2	11.6
Eucyclogobius newberryi (R)	0.1	0.1	—	—
Gasterosteus aculeatus (F)	0.9	1.5	0.2	0.3
Gillichthys mirabilis (R)	—	—	2.4	3.9
Gobiidae	—	—	1.9	3.1
Hyperprosopon argenteum (MI)	<0.1	<0.1	—	—
Hypomesus pretiosus (M)	1.3	2.3	—	—
Hypsopsetta guttulata (MI)	—	—	<0.1	<0.1
Lepidogobius lepidus (R)	1.0	1.7	—	—
Leptocottus armatus (R)	14.0	23.7	2.2	3.5
Mugil cephalus (R)	—	—	0.1	0.1
Paralichthys californicus (MI)	—	—	0.1	0.1
Phanerodon furcatus (PR)	0.2	0.3	—	—
Platichthys stellatus (MI)	13.0	22.0	<0.1	<0.1
Porichthys notatus (MI)	1.1	1.8	0.7	1.1
Syngnathus leptorhynchus (R)	1.0	1.8	—	—
Triakis semifasciata (PR)	—	—	0.1	0.1
Urolophus halleri (M)	<0.1	0.1	—	—
Mean number of fish sample^{-1}	59.1		62.1	
Total number of fish	5,074		3,352	
Number of species	20		16	
Number of samples	86		54	

these species no longer were in the slough by the following fall. These fishes may enter the slough in summer or become available to collection gear after being spawned in the slough during spring and summer. For example, the abundance and distribution of *Parophrys vetulus* (English sole) were distinctly seasonal, with a steady increase in abundance of juveniles at all stations in the main channel during spring, and a peak at the Kirby Park station in summer (mean length = 76 mm SL). *Parophrys vetulus* was not taken from the Kirby Park station during fall months, but increased in abundance at the ocean station during that period (mean SL = 134 mm).

A total of 5,074 fishes was collected by beach seine (n = 86 samples) in Bennett Slough from August 1974 to August 1976 (Table 5). Although the total number of species (20) was relatively low, average density (59.1 fish per sample) was high. Three euryhaline species, *C. ios*, *L. armatus*, and *Platichthys stellatus* (starry flounder), were most abundant and accounted for 80.6% of the total catch (Table 4). *Leptocottus armatus* and *P. stellatus* were collected from Bennett Slough in all months of the year; *C. ios* were not collected during winter.

Clevelandia ios was the most numerous species in Bennett Slough, contributing 34.9% of the total catch and numerically dominating (59%) the catch in summer months. This gobiid also ranked second in beach seine and channel net collections from the tidal creeks and the Hudson's Landing station in upper Elkhorn Slough (Table 5). In contrast, *C. ios* ranked 22 of 42 species and contributed only 0.3% to the overall catch from otter trawls taken throughout Elkhorn Slough. This species was essentially absent from the ocean, lower, and middle slough otter trawl collections and was collected only in low numbers in trawls at the tidal creeks and Hudson's Landing stations (Table 1).

Like *C. ios*, *L. armatus* was most abundant in Bennett Slough during summer months (32% of the catch); those collected in summer were immature and <120 mm SL. During spring, maximum mean length of *L. armatus* was 149 mm SL, which is larger than the size at first maturity (120 mm TL; Jones 1962). *Platichthys stellatus* dominated (60%) the catch

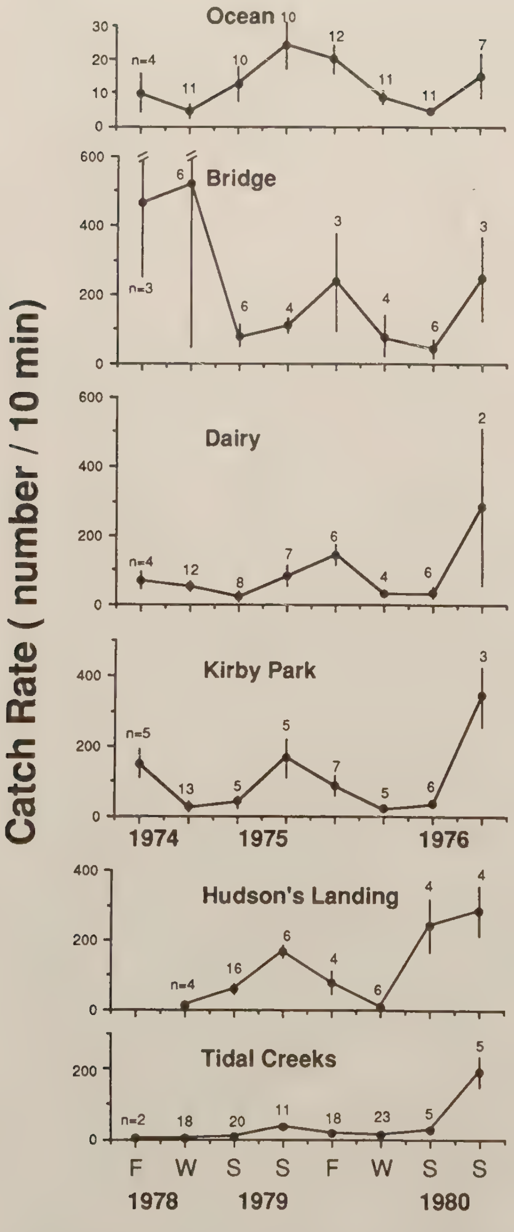

Fig. 2. Seasonal variation in mean catch (number per 10-min tow) of fish from otter trawls at each location in Elkhorn Slough, California; data from Long Canyon and Rubis Creek were combined into one tidal creek location. Vertical bars indicate standard errors. Number of samples (n) is indicated above data points.

during winter, and its mean standard length ranged from 33 mm in June to 258 mm in March. Because length at maturity is about 300 mm SL for males and 350 mm SL for females (Orcutt 1950), all *P. stellatus* taken in Bennett Slough were immature.

Although catch rates from seine collections in Bennett Slough are not comparable directly to those from otter trawls in Elkhorn Slough, relative abundance and species composition can be evaluated between the two sloughs. The majority of the fishes found in Bennett Slough also were common in Elkhorn Slough, even though indices of similarity between the two sites were low (Table 3). Species similarity increased with distance inland, and was greatest between the Bennett Slough assemblage and those at the tidal creek and Hudson's Landing stations, primarily because of the numerical dominance of *L. armatus* and *P. stellatus*. Dominance indices were highest for fish assemblages at the Bennett Slough and Hudson's Landing stations; only three species represented >80% of the total fish abundance at these stations (Table 4). Species assemblages were least similar between Bennett Slough and the ocean station.

Notably, *Acanthogobius flavimanus* (yellowfin goby), a euryhaline species introduced from Japan (Brittan et al. 1970), and *Gasterosteus aculeatus* (three-spine stickleback), primarily a freshwater species, were only collected by beach seines in Bennett Slough and the most shallow areas of Elkhorn Slough (Table 5). *Cottus asper* (prickly sculpin), also a freshwater species, *Eucyclogobius newberryi* (tidewater goby), and juvenile (<50 mm SL) *Hypomesus pretiosus* (surf smelt), a marine species only found as larvae in Elkhorn Slough (Yoklavich et al. 1992), were collected only in Bennett Slough regardless of sampling gear. As in Elkhorn Slough, species richness in Bennett Slough was low in winter and early spring (mean of six species per haul) and high in summer and early fall (a mean of 10–11 species per haul).

The ichthyofauna in otter trawl collections from Elkhorn Slough included a large number of marine species (Table 6), ranging from 55% to 66% of upper and lower slough species, respectively. About half of the marine species in the lower slough were marine immigrants (or slough opportunists) and the rest were uncommon species from nearshore habitats. Over 70% of the marine species in the upper slough were marine immigrants, using the slough as spawning and nursery grounds. Marine immigrants contributed from 21.5% to 32.3% of the total number of fishes collected throughout the slough. The relative abundance of strictly marine fishes declined from 2.7% in the lower slough to 0.6% in the upper slough.

Resident and partial-resident species occurred

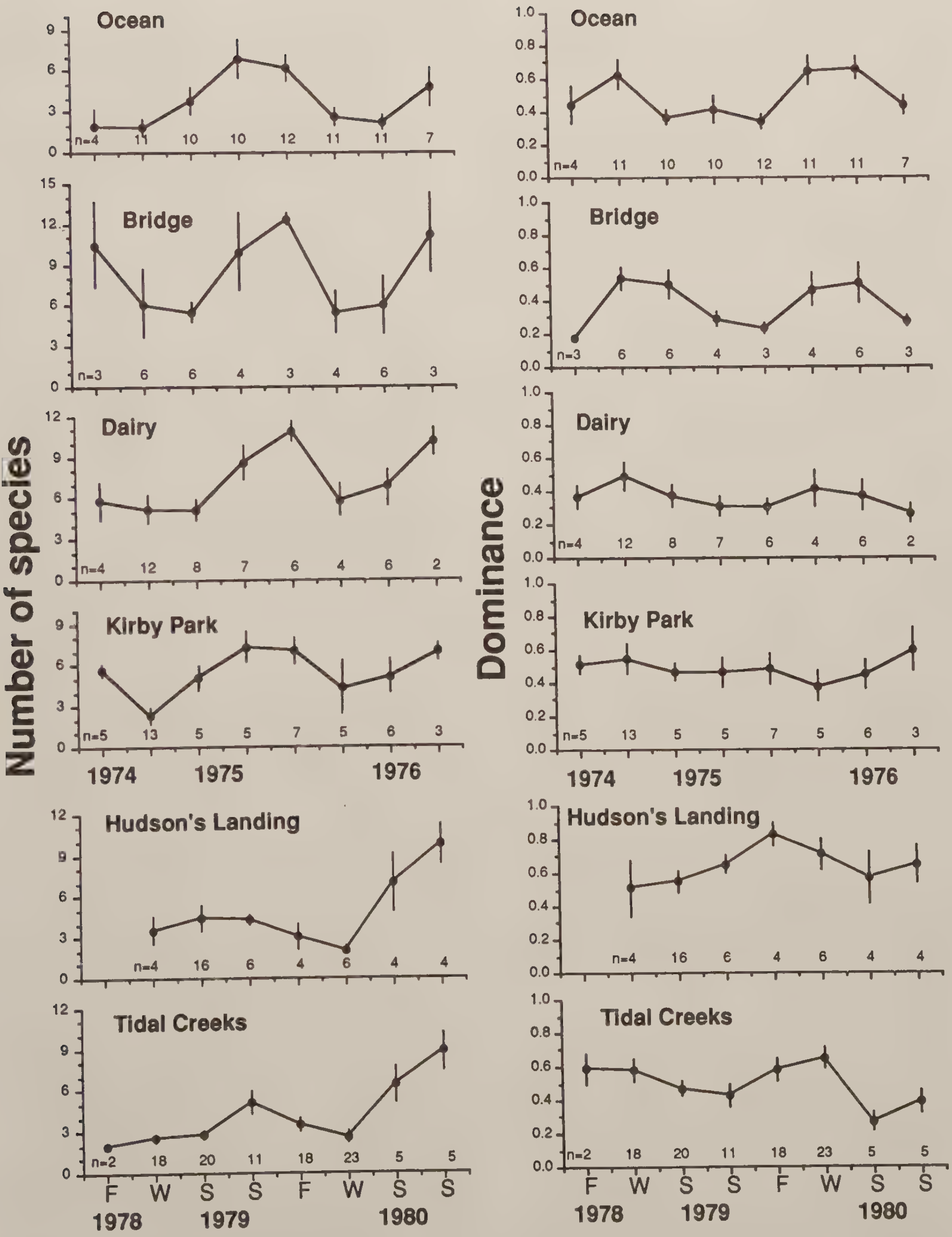

Fig. 3. Seasonal variation in diversity (mean number of species and mean dominance index per 10-min tow) of fish from otter trawls at each location in Elkhorn Slough, California; data from Long Canyon and Rubis Creek were combined into one tidal creek location. Vertical bars indicate standard errors. Number of samples (n) is indicated above data points.

TABLE 6. Number and percentage of species and individuals contributing to each life-style category from otter trawl collections of fishes taken in the lower (bridge and dairy stations), middle (Kirby Park station), and upper (Hudson's Landing and tidal creek stations) regions of Elkhorn Slough and from beach seine collections of fishes taken in Bennett Slough. Only species >0.1% of total abundance were evaluated.

	Elkhorn Slough							
	Lower		Middle		Upper		Bennett Slough	
Life-style Category	Number	Percent	Number	Percent	Number	Percent	Number	Percent
Species								
Marine	10	30.3	3	12.0	5	16.1	2	10.0
Marine immigrant	12	36.4	12	48.0	12	38.7	5	25.0
Slough resident	5	15.2	3	12.0	6	19.4	7	35.0
Partial resident	6	18.2	6	24.0	6	19.4	4	20.0
Freshwater	—	—	1	4.0	2	6.5	2	10.0
Total	33		25		31		20	
Individuals								
Marine	285	2.7	27	0.7	41	0.6	122	2.4
Marine immigrant	2,273	21.5	925	24.3	2,264	32.3	1,279	25.2
Slough resident	1,681	15.9	628	16.5	3,972	56.7	3,308	65.2
Partial resident	6,331	59.9	2,197	57.7	666	9.5	289	5.7
Freshwater	—	—	30	0.8	47	0.7	76	1.5
Total	10,570		3,807		6,990		5,074	

throughout the slough in equal proportions. The proportion of the total number of resident fishes increased from 15.9% in the lower slough to 56.7% in the upper slough. Numbers of fishes with partial-resident status were exceptionally high (58–60%) in the lower and middle regions, largely due to *C. aggregata* (this species is found in all but some winter months). Freshwater species were found only in the middle and upper slough regions.

Over 70% of the total number of fishes collected in Bennett Slough, represented by 11 species (55% of the total number of species), were categorized as resident and partial-resident slough species (Table 6). The relative number of resident species (35%) and proportion of total individuals (65.2%) was higher here than at any location in Elkhorn Slough. Marine and freshwater species each comprised only 10% of all species, representing 2.4% of the total catch. The proportion of marine immigrant individuals was comparable to that in Elkhorn Slough, but this category included fewer species in Bennett Slough.

Discussion

The ichthyofauna of Elkhorn Slough is characterized by a few dominant species that reside year-round within the system or leave only for brief periods, and several seasonally dominant species that enter the slough as reproductively active adults or as juveniles. Seasonal and spatial variations in abundance, species richness, and distribution of fish assemblages in Elkhorn Slough and adjacent habitats are similar to patterns described for other estuarine systems. Higher abundance and species richness during the summer invasion of young-of-the-year marine species into the slough also have been documented for fish assemblages in other temperate bays and estuaries, and were positively correlated with temperature (Allen and Horn 1975; Hoff and Ibara 1977; Allen 1982; Onuf and Quammen 1983). The decline in species richness and change in species composition with distance up Elkhorn Slough has been noted in other systems as well (Loneragan et al. 1986; Blaber et al. 1989). The lower slough is strongly influenced by marine hydrographic processes (Broenkow 1977), and therefore more accessible to coastal marine species. Dominant species of the upper slough and tidal creeks are best characterized as euryhaline, with affinities toward higher temperature. Higher temperature, nutrient content, and residence time of water above the tidal prism (approximately east of the dairy station; Smith 1973) enhance production of food for fishes in the upper slough and tidal creeks, but may exclude less thermally-tolerant marine species during some seasons.

Although species composition may vary latitudinally, the numerically dominant fishes in estuaries along the west coast of the United States are juvenile members of similar trophic levels (planktivores or low-level carnivores on infaunal invertebrates) and families (Atherinidae, Bothidae, Cottidae, Embiotocidae, Engraulidae, Gobiidae, Pleuronectidae). According to cluster analyses of Horn and Allen (1976), species composition of Elkhorn Slough fish assemblages is most similar to that of Morro Bay, and defines a unique faunal group for central California bays. More generally, fish assemblages of bays north of Point Conception were distinguished from those of southern California (Horn and Allen 1976).

The maximum number of species found in any of these systems may be influenced by the surface area of the estuarine system (Horn and Allen 1976), as well as the structural complexity of the habitat (Weinstein and Brooks 1983; Weinstein 1985). The smaller tidal creeks and upper Elkhorn Slough stations supported fewer species than did the wide main channel with larger expanses of sand and mud bottom. Although Elkhorn Slough generally lacks the abundant submerged vegetation prevalent in other estuaries, the increased heterogeneity of habitat at the lower slough stations (due to submerged rocks and pilings, and commercial oyster racks) was accompanied by increased species richness. Recent restoration of temperate seagrass beds (*Zostera marina*) in Elkhorn Slough could increase species diversity, and modify the distribution and trophic structure of slough ichthyofauna to include more detritivores and epifaunal consumers (Whitfield 1988). Moreover, because survival during early life often delimits year-class success for marine fishes, increased availability of spawning substrate from eelgrass could enhance recruitment for those species with demersal adhesive eggs.

The characterization of fish assemblages in shallow bays often is confounded by the biases associated with collection techniques, which vary with season, location, and life stage of the fish (Weinstein and Davis 1980; Allen 1982; Horn and Allen 1985; Pierce et al. 1990). Avoidance of towed nets, such as otter trawls, by the largest, most active fishes (e.g., *Triakis semifasciata, Mustelus* spp. [smoothhounds], and *Morone saxatilis* [striped bass]), and by the adults of many schooling fishes (e.g., *Clupea pallasii, Engraulis mordax,* and the atherinids) contributes to the underestimation of abundance of these species, and likewise inflates the relative importance of gear-susceptible species. *Atherinops affinis* and *Atherinopsis californiensis* clearly were under represented in otter trawl collections, as indicated by the increased relative abundance in beach seine and channel net collections (Table 5) and in gill net collections (Ruagh 1976). Indeed, *A. affinis* contributed significantly to secondary production estimated from beach seine collections taken in a southern California estuary (Allen 1982). Extrusion of small adults (e.g., *E. mordax*) and juveniles from towed nets also results in an underestimate of their abundance. Otter trawls are inadequate to sample many members of Gobiidae, including the common residents *Clevelandia ios, Gillichthys mirabilis,* and *Acanthogobius flavimanus.* These species burrow in sand and mud substrate when disturbed, potentially avoiding the trawl, and often are more abundant in shallow areas where trawling is impractical. Interestingly, typical slough species (*Leptocottus armatus, Platichthys stellatus, Phanerodon furcatus, Embiotoca jacksoni, Cymatogaster aggregata,* and *Hyperprosopon argenteum*) dominated creel census data collected throughout Elkhorn and Bennett Sloughs during our study (Cailliet et al. 1977). As expected from the otter trawl collections, *Psettichthys melanostictus* was commonly caught only by fishermen near the entrance of the slough on the harbor jetties.

Regardless of potential gear biases, Elkhorn Slough is important to several species of fishes as spawning and nursery grounds, as well as a permanent home to at least six resident species. Large numbers of juvenile *Parophrys vetulus,* classified as a marine immigrant, were collected at all stations during the spring and summer months. This commercially important species relies heavily on larger northern estuarine systems as nursery grounds (e.g., Gray's Harbor and Willapa Bay, Washington [Gunderson et al. 1990], Yaquina Bay, Oregon [Pearcy and Myers 1974; Krygier and Pearcy 1986] and Humboldt Bay, California [Toole 1980]), and conspicuously is missing from ichthyofaunal surveys of more southern bays (Horn and Allen 1985). Yoklavich (1982) suggested that Elkhorn Slough is the most southern bay used significantly as a nursery by juvenile *P. vetulus,* and that the occurrence of this species in shallow inshore areas may be limited by ontogenetic changes in thermal tolerance.

Most other flatfish species, including *Citharichthys stigmaeus, Paralichthys californicus* (California halibut), and *Platichthys stellatus,* also were considered marine immigrants and occurred as juveniles in larger numbers at the stations closest to the entrance to Elkhorn Slough. All *Sebastes,* which are viviparous marine fishes that spawn offshore, occurred only as juveniles at the near-ocean stations. Spawning *Porichthys notatus* (plainfin midshipman) were relatively abundant in Bennett Slough and at the Kirby Park station in Elkhorn Slough during the spring, and their young were abundant especially in protected areas of Bennett Slough. At least seven species of embiotocids released live young in the slough; three species (i.e., *Cymatogaster aggregata, Phanerodon furcatus,* and *Embiotoca jacksoni*) were among the dominant species and were classified as residents and partial residents. Several viviparous species of elasmobranchs, categorized as partial-residents, occur almost year-round and spawn in Elkhorn Slough (Talent 1985). Egg masses, larvae and juveniles of *Clupea pallasii* and the family Atherinidae were abundant seasonally in Elkhorn Slough (Ruagh 1976; Yoklavich et al. 1992), despite the likely underestimation of adult abundance.

The distinct seasonal distribution and abundance of several species can be attributed largely to their reproductive habits. Time of spawning influences the spatial and temporal coincidence of larval and juvenile distributions in the slough. The increase in abundance of juvenile *Clupea pallasii* in upper areas of the slough during spring is consistent with spawning on eelgrass in bays and estuaries along the central California coast during winter months (Miller and Schmidtke 1956). The high abundance of the three dominant species of embiotocids (*C. aggregata, E. jacksoni,* and *P. furcatus*) in summer and early fall reflects their summer spawning (Antrim 1981). Their microdistributional patterns within the slough also are related to their reproductive habits, with *C. aggregata* (the numerically dominant species in Elkhorn Slough) entering upper areas of the slough to spawn (Barry 1983) and *P. furcatus* (third dominant overall) spawning at the lower stations (Antrim 1981). *Embiotoca jacksoni* (fourth dominant species and classified as a resident) concentrated as adults and juveniles in the main channel of the lower slough, although both were collected in low numbers at the shallow upper slough stations. Notably, *E. jacksoni* occurs on shallow rocky reefs off southern California (Hixon 1979; Schmitt and Holbrook 1990), but is considered a member of bay and estuarine ichthyofauna closer to its northern geographical margin (Fort Bragg in northern California).

The winter decline in fish abundance and species richness can be attributed to many of the partial-resident species leaving the slough during this time, including *C. aggregata, T. semifasciata,* and young *Myliobatis californica.* Notably, this decline occurred during years of relatively normal rainfall (1974–1975) and virtually no rainfall (1975–1976). The resident species that remain in the slough throughout the year are generally euryhaline fishes. Higher dominance indices in winter in Elkhorn Slough are not consistent with results from studies in southern California bays, where high summer dominance coincided with increased abundance of a few species of migratory fishes (e.g., *Engraulis mordax*; Allen 1982; Horn and Allen 1985). In Elkhorn Slough, the trend toward higher dominance indices in the winter, especially in the tidal creeks, reflects the high number of young *Leptocottus armatus*; this resident species spawns in the winter in Elkhorn Slough, and larvae are abundant throughout the slough (Yoklavich et al. 1992).

The role that estuaries and bays play in the life cycle of coastal marine fishes is difficult to assess. The high relative abundance of marine-related (i.e., marine, marine immigrant, and partial-resident life style categories) individuals and species entering Elkhorn Slough early in life or as spawning adults demonstrates the importance of this habitat to nearshore fish communities. Relatively large numbers of marine immigrants, especially in the highly productive shallow tidal creeks and upper areas of the slough, can function to transport energy from nursery habitats to offshore waters. The occurrence of few habitats such as Elkhorn Slough along the central California coast implies that remaining areas are important to the success of nearshore marine fishes.

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Literature Cited

Allen, L. G. 1982. Seasonal abundance, composition, and productivity of the littoral fish assemblage in upper Newport Bay, California. *Fishery Bulletin U.S.* 80:769–790.

Allen, L. G. and M. H. Horn. 1975. Abundance, diversity and seasonality of fishes in Colorado Lagoon, Alamitos Bay, California. *Estuarine and Coastal Marine Science* 3:371–380.

Ambrose, D. A. 1976. The distribution, abundance, and feeding ecology of four species of flatfish in the vicinity of Elkhorn Slough, California. M.A. Thesis, San Jose State University, San Jose, California. 121 p.

Antrim, B. S. 1981. Habitat and food resource utilization of three species of embiotocids in Elkhorn Slough, Monterey Bay, California. M.A. Thesis, California State University, Fresno, California. 86 p.

Appiah, J. C. 1977. Species composition and abundance of fish populations in Bennett Slough, Monterey Bay, California. M.A. Thesis, California State University, Fresno, California. 63 p.

Barry, J. P. 1983. Utilization of shallow marsh habitats by fishes in Elkhorn Slough, California. M.A. Thesis, San Jose State University, San Jose, California. 95 p.

Barry, J. P. and G. M. Cailliet. 1981. The utilization of shallow marsh habitats by commercially important fishes in Elkhorn Slough, California. *Cal-Neva Wildlife Transactions* 1981:38–47.

Blaber, S. J. M., D. T. Brewer, and J. P. Salini. 1989. Species composition and biomasses of fishes in different habitats of a tropical northern Australian estuary: Their occurrence in the adjoining sea and estuarine dependence. *Estuarine, Coastal and Shelf Science* 29:509–531.

Bozeman, E. L., Jr. and J. M. Dean. 1980. The abundance of estuarine larval and juvenile fish in a South Carolina intertidal creek. *Estuaries* 3:89–97.

Brittan, M. R., J. D. Hopkirk, J. D. Conners, and M. Martin. 1970. Explosive spread of the oriental goby *Acanthogobius* *flavimanus* in the San Francisco Bay-Delta region of California. *Proceedings of the California Academy of Science, 4th Series* XXXVIII:207–214.

Broenkow, W. 1977. Water chemistry of Elkhorn Slough and Moss Landing Harbor, p. 387–464. *In* J. Nybakken, G. Cailliet, and W. Broenkow (eds.), Ecologic and Hydrographic Studies of Elkhorn Slough Moss Landing Harbor and Nearshore Coastal Waters. Moss Landing Marine Laboratories Technical Publication, Moss Landing, California.

Browning, B. M. 1972. The natural resources of Elkhorn Slough: Their present and future use. *California Department of Fish and Game, Coastal Wetlands Series 4.* 105 p.

Cailliet, G. M. and J. P. Barry. 1978. Comparison of food array overlap measures useful in fish feeding habit analysis, p. 67–79. *In* S. J. Lipovsky and C. A. Simenstad (eds.), Fish Food Habits Studies, Proceedings of the Second Pacific Northwest Technical Workshop. Washington Sea Grant WSG-WO-77-2.

Cailliet, G. M., B. Antrim, D. Ambrose, S. Pace, and M. Stevenson. 1977. Species composition, abundance and ecological studies of fishes, larval fishes, and zooplankton in Elkhorn Slough, p. 216–386. *In* J. Nybakken, G. Cailliet, and W. Broenkow (eds.), Ecologic and Hydrographic Studies of Elkhorn Slough Moss Landing Harbor and Nearshore Coastal Waters. Moss Landing Marine Laboratories Technical Publication, Moss Landing, California.

Dando, P. R. 1984. Reproduction in estuarine fish, p. 155–170. *In* G. W. Potts and R. J. Wootton (eds.), Fish Reproduction Strategies and Tactics. Academic Press, London.

Darnell, R. M. and T. M. Soniat. 1979. The Estuary/Continental Shelf as an Interactive System. Ecological Processes in Coastal and Marine Systems. Plenum Press, New York. 548 p.

Day, J. W., Jr. and A. Yanez-Arancibia. 1985. Coastal lagoons and estuaries as an environment for nekton, Chap. 3, p. 17–34. *In* A. Yanez-Arancibia (ed.), Fish Community Ecology in Estuaries and Coastal Lagoons: Toward an Ecosystem Integration. DR (R) UNAM Press Mexico, Mexico City.

Gunderson, D. R., D. A. Armstrong, Y.-B. Shi, and R. A. McConnaughey. 1990. Patterns of estuarine use by juvenile English sole (*Parophrys vetulus*) and Dungeness crab (*Cancer magister*). *Estuaries* 13:59–71.

Hixon, M. A. 1979. Competitive interactions and spatio-temporal patterns among California reef fishes of the genus *Embiotoca.* Dissertation, University of California, Santa Barbara. 213 p.

Hoff, J. G. and R. M. Ibara. 1977. Factors affecting the seasonal abundance, composition and diversity of fishes in a southeastern New England estuary. *Estuarine and Coastal Marine Science* 5:665–678.

Horn, M. H. and L. G. Allen. 1976. Numbers of species and faunal resemblance of marine fishes in California bays and estuaries. *Bulletin of the Southern California Academy of Science* 75:159–170.

Horn, M. H. and L. G. Allen. 1985. Fish community ecology in southern California bays and estuaries, Chap. 8, p. 169–190. *In* A. Yanez-Arancibia (ed.), Fish Community Ecology in Estuaries and Coastal Lagoons: Toward an Ecosystem Integration. DR (R) UNAM Press Mexico, Mexico City.

Jones, A. C. 1962. The biology of the euryhaline fish *Leptocottus armatus* Girard (Cottidae). *University of California Publications in Zoology* 67:321–368.

Krebs, C. J. 1989. Ecological Methodology. Harper and Row, Publishers, New York. 654 p.

Krygier, E. E. and W. G. Pearcy. 1986. The role of estuarine and offshore nursery areas for young English sole, *Parophrys vetulus* Girard, off Oregon. *Fishery Bulletin U.S.* 84:119–132.

Lenanton, R. C. J. and I. C. Potter. 1987. Contribution of estuaries to commercial fisheries in temperate western Australia and the concept of estuarine dependence. *Estuaries* 10: 28–35.

Loneragan, N. R., I. C. Potter, R. C. J. Lenanton, and N. Caputi. 1986. Spatial and seasonal differences in the fish fauna in the shallows of a large Australian estuary. *Marine Biology* 92:575–586.

Loneragan, N. R., I. C. Potter, and R. C. J. Lenanton. 1989. Influence of site, season and year on contributions made by marine, estuarine, diadromous and freshwater species to the fish fauna of a temperate Australian estuary. *Marine Biology* 103:461–479.

McGowan, M. F. 1986. Northern anchovy, *Engraulis mordax,* spawning in San Francisco Bay, California, 1978–79, relative to hydrography and zooplankton prey of adults and larvae. *Fishery Bulletin U.S.* 84:879–894.

Miller, D. J. and J. Schmidtke. 1956. Report on the distribution and abundance of Pacific herring (*Clupea pallasii*) along the coast of central and southern California. *California Fish and Game* 42:163–186.

NOAA (National Oceanic and Atmospheric Administration). 1990. Distribution and abundance of fishes and invertebrates in west coast estuaries, Vol. 1: Data summaries. Strategic Assessment Branch, NOS/NOAA, Rockville, Maryland. 240 p.

Odum, W. E. and E. J. Heald. 1975. The detritus-based foodweb of an estuarine mangrove community, p. 265–286. *In* L. E. Chronin (ed.), Estuarine Research. Academic Press, New York.

Onuf, C. P. and M. L. Quammen. 1983. Fishes in a California coastal lagoon: Effects of major storms on distribution and abundance. *Marine Ecology Progress Series* 12:1–14.

Onuf, C. P., M. L. Quammen, G. P. Shaffer, C. H. Peterson, J. W. Chapman, J. Cermak, and R. W. Holmes. 1978. An analysis of the values of central and southern California coastal wetlands, p. 186–199. *In* P. W. Greeson, J. R. Clark, and J. E. Clark (eds.), Wetland Functions and Values: The State of our Understanding. American Water Resources Association, Minneapolis, Minnesota.

Orcutt, H. G. 1950. The life history of the starry flounder, *Platichthys stellatus* (Pallas). *California Fish and Game Fish Bulletin* 78:1–64.

Pearcy, W. G. and S. S. Myers. 1974. Larval fishes of Yaquina Bay, Oregon: A nursery ground for marine fishes? *Fishery Bulletin U.S.* 72:201–213.

Pierce, C. L., J. B. Rasmussen, and W. C. Leggett. 1990. Sampling littoral fish with a seine: Corrections for variable capture efficiency. *Canadian Journal of Fisheries and Aquatic Sciences* 47:1004–1010.

Rosenberg, A. A. 1982. Growth of juvenile English sole, *Parophrys vetulus,* in estuarine and open coastal nursery grounds. *Fishery Bulletin U.S.* 80:245–252.

Ruagh, A. A. 1976. Feeding habits of silversides (family Atherinidae) in Elkhorn Slough, Monterey Bay, California. M.A. Thesis, California State University, Fresno, California. 60 p.

Schmitt, R. J. and S. J. Holbrook. 1990. Population responses of surfperch released from competition. *Ecology* 71: 1653–1665.

Shenker, J. M. and J. M. Dean. 1979. The utilization of an intertidal salt marsh creek by larval and juvenile fishes: Abundance, diversity and temporal variation. *Estuaries* 2:154–163.

Smith, R. E. 1973. The hydrography of Elkhorn Slough, a shallow California coastal embayment. Moss Landing Marine Laboratories Technical Publication 73-2, Moss Landing, California. 88 p.

Talent, L. G. 1985. The occurrence, seasonal distribution, and reproductive condition of elasmobranch fishes in Elkhorn Slough, California. *California Fish and Game* 71:210–219.

Toole, C. L. 1980. Intertidal recruitment and feeding in relation to optimal utilization of nursery areas by juvenile English sole (*Parophrys vetulus*). *Environmental Biology of Fishes* 5: 383–390.

WANG, J. C. S. 1981. Taxonomy of the Early Life Stages of Fishes—Fishes of the Sacramento-San Joaquin Estuary and Moss Landing Harbor-Elkhorn Slough, California. Ecological Analysts, Inc., Concord, California. 168 p.

WEINSTEIN, M. P. 1979. Shallow marsh habitats as primary nurseries for fishes and shellfish, Cape Fear River, North Carolina. *Fishery Bulletin U.S.* 77:339–357.

WEINSTEIN, M. P. 1981. Plankton productivity and the distribution of fishes on the southeastern U.S. continental shelf. *Science* 214:351–352.

WEINSTEIN, M. P. 1985. Distributional ecology of fishes inhabiting warm-temperate and tropical estuaries: Community relationships and implications, Chap. 14, p. 285–310. *In* A. Yanez-Arancibia (ed.), Fish Community Ecology in Estuaries and Coastal Lagoons: Toward an Ecosystem Integration. DR (R) UNAM Press Mexico, Mexico City.

WEINSTEIN, M. P. AND H. A. BROOKS. 1983. Comparative ecology of nekton residing in a tidal creek and adjacent seagrass meadow: Community composition and structure. *Marine Ecology Progress Series* 12:15–27.

WEINSTEIN, M. P. AND R. W. DAVIS. 1980. Collection efficiency of seine and rotenone samples from tidal creeks, Cape Fear River, North Carolina. *Estuaries* 3:98–105.

WHITFIELD, A. K. 1988. The fish community of the Swartvlei estuary and the influence of food availability on resource utilization. *Estuaries* 11:160–170.

YOKLAVICH, M. M. 1982. Growth, food consumption, and conversion efficiency of juvenile English sole (*Parophrys vetulus*), p. 97–105. *In* G. M. Cailliet and C. A. Simenstad (eds.), Fish Food Habit Studies, Proc. Third Pacific Workshop. University of Washington, Washington Sea Grant.

YOKLAVICH, M. M., M. STEVENSON, AND G. M. CAILLIET. 1992. Seasonal and spatial patterns of ichthyoplankton abundance in Elkhorn Slough, California. *Estuarine, Coastal and Shelf Science* 34:1–18.

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